PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

VOL. IV JULY, 1950 NO. 3

Previous issue published April 28, 1950

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PACIFIC SCIENCE, a quarterly publication of the University of Hawaii, appears in January, April, July, and October. Subscription price is three dollars a year; single copies are one dollar. Check or money order payable to University of Hawaii should be sent to PACIFIC SCIENCE, Office of Publication, University of Hawaii, Honolulu 14, Hawaii. Reprints of articles from Volumes I and II are available to subscribers.

The Antibacterial Properties of Some Plants Found in Hawaii

O. A. Bushnell, Mitsuno Fukuda, and Takashi Makinodan[1]

Many of the plants, both indigenous and introduced, which now grow in Hawaii have been used for medicinal purposes by the native Hawaiians and by the people of other countries who have come to live in Hawaii. When, in 1934, Handy, Pukui, and Livermore made their survey of the Hawaiian pharmacopeia, they were able to distinguish 317 different botanical components in the catalogue of ingredients used until that time. It is probable that many other species of plants which are sources of favorite remedies in other countries have been imported to Hawaii and could be added to the list prepared by Handy and his coworkers (1934), who were concerned primarily with remedies used by the native Hawaiians.

The Hawaiian remedies, especially those derived from the lore of the *kahuna lapaau laau*, the herb doctor of the ancient Hawaiians, have been much praised but they have never been critically appraised; and we thought that perhaps we could gain some idea of their relative value if we studied the medicinal plants from which these remedies were prepared for evidences of the antibacterial properties they might possess.

Most of the plants we set out to study were chosen from the native Hawaiian *materia medica*, but we did not exclude plants used for medicinal purposes by people of other ethnic groups. In some instances, moreover, we studied imported plants which were related to the species considered to be of value by the Hawaiians, even though the imported plants were not themselves mentioned in the accounts we consulted in preparing our own list of plants to be investigated.

Our list was compiled from several publications discussing Hawaiian pharmaceutics (Kaaiakamanu and Akina, 1922; Degener, 1930; Handy, Pukui, and Livermore, 1934; Neal, 1948); from suggestions given us by a Hawaiian herbalist on plants in current usage; and from hearsay and our own personal experience with plants used by Japanese, Chinese, and other ethnic groups in Hawaii. In preparing this list, those plants which appear to have been used against bacterial infections were selected wherever identification of the plant had been established and whenever it was likely that we would be able to find it in order to test it. The more common or the more famous of the medicinal plants were also included in the list, even if they had been employed to treat conditions obviously having no bacterial etiology. Our list, then, is a heterogeneous one, by no means confined to the native Hawaiian plants, and contains more than 275 entries.

When we began these studies we expected to be able, in time, to study all the plants in our list, and therefore were not particularly concerned about the order in which we collected them, taking them in the haphazard sequence in which we found them; but now the pressure of other duties makes it evident that we shall not be able to finish the studies as we had planned. Rather than lose the information we have obtained, therefore, we are recording in this paper the data from our observations on the 101 medicinal plants we were able to investigate before our studies were forced to an end.

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METHODS

The method of measuring the antibacterial properties of plants is essentially the same as that devised by the Oxford group (Abraham *et al.*, 1941) for assaying penicillin and since adapted to the assay of other antibiotics produced by micro-organisms. It is a method which has been used in other parts of the world to appraise medicinal plants (Pederson and Fisher, 1944; Lucas and Lewis, 1944; Sanders, Weatherwax, and McClung, 1945; Carlson *et al.*, 1946; and many others). It is based upon the assumption that an agent which acts upon a test organism to achieve a particular effect will also act upon other related organisms in a similar manner. While the assumption is not always substantiated by experimental evidence, it is tenable often enough to give the method some usefulness as a "screening test" for distinguishing agents that are "likely" to be effective from those which are "likely" to be ineffective. It is a method which has its deficiencies, certainly, but it is better than no method at all.

The plants to be studied were collected over a period of 2 years as they could be found on the island of Oahu. Most of them were obtained on or near the University of Hawaii campus and in the adjacent Manoa Valley. Whenever feasible, specimens of the complete plant—roots, stems, leaves, buds, flowers, and fruits—were obtained, either all at once or during those seasons when they could be found. In the case of a plant of which only certain portions had been used in the native pharmacopeia, we were careful to collect and to study at least those prescribed portions of the plant if not all of it. Many of the plants, or many of the parts of the different species, were tested several times during the course of our study, in several instances by each of us independently.

The specimens were taken to the laboratory soon after they were collected, and either were subjected immediately to the process of assay or were frozen and held at −10° C. until they could be studied.

Extracts of the whole plants or of certain separated portions of them—as, for example, the roots, the stems, the leaves, the flowers, the fruits, or of any indicated combinations of these—were obtained by first cutting the plant material into small pieces and by then subjecting these fragments to high pressures, ranging from 15,000 to 20,000 pounds per square inch, achieved by means of a Carver hydraulic press. No water or solvent of any kind was added to the plant material, and in almost all cases the specimens yielded ample amounts of tissue fluids for the purposes of the study.

The extracts of the different portions of the plants were kept in separate beakers, and were placed immediately in a refrigerator until the next step in the assay could be performed. In most instances the period of storage was only 1 to 2 hours; in no case was it longer than 4 hours.

Most of the extracts were assayed for their antibacterial effect upon three test strains of bacteria: *Micrococcus pyogenes* var. *aureus* (until recently known as *Staphylococcus aureus*), *Escherichia coli*, and *Pseudomonas aeruginosa*. A few of those extracts studied early in these investigations were tested against *M. pyogenes* var. *aureus* and *E. coli* only. Seventeen of the plants, which the literature described as having been employed to combat intestinal infections, were tested against five different strains of enteric pathogens as well as against the three standard cultures. The enteric pathogens used were: *Salmonella typhosa, Sal. montevideo, Sal. schottmuelleri, Shigella paradysenteriae* BH, and *Shig. paradysenteriae* III-Z. Cultures of all of these test organisms were obtained from the stock culture collection of the Department of Bacteriology, University of Hawaii.

Pure cultures of the test bacteria were grown in nutrient broth at 37° C. for 24 hours before they were used. When an assay

was about to be performed, 0.5 ml. of the broth culture of the test organism was inoculated into 100 ml. of melted nutrient agar cooled to 41° C. This heavily seeded agar medium was then poured into sterile petri dishes, about 10 ml. to a dish, and the medium was allowed to solidify at room temperature. After the medium had solidified, one or two sterile porcelain penicups were placed upon the surface of the agar.

The plant extract being tested was then placed in the appropriate penicup, 0.2 ml. of extract in each cylinder. At first extracts were tested in duplicate until, with time and the perfection of our techniques, we found that duplicate platings were unnecessary. The plates were incubated in the upright position at 37.5° C. for 24 hours, at which time they were examined for the degree of inhibition achieved by the plant extracts as they diffused into the medium from the bases of the penicups. In most of the instances in which inhibition was achieved, it was denoted by a clear halo-like zone in the medium around the penicup, with the heavy growth of uninhibited bacteria making the medium opaque around the periphery of the zone of inhibition. A few of the plant extracts produced a considerable discoloration or opacity in the medium around the penicups, but in only a very few instances did this discoloration interfere with determinations of the extracts' effects upon the test organisms.

The degree of antibacterial effect was reflected directly, of course, in the size of the zone of inhibition: the greater the zone, the more potent the extract. The diameter of the zone could be measured quite easily in most instances and was recorded, in millimeters, for each extract tested.

Several other techniques for determining the efficacy of the plant extracts were also tried—such as using filter paper discs of varying sizes soaked in the plant extract before they were applied to the inoculated agar, or actually incorporating 1 ml. of the plant extract or of varying dilutions of it into the inoculated medium before it had solidified—but the penicup method seemed to be the one which gave the most consistent and the most clear-cut results, and it was adopted for continued use.

Just before each extract was tested for its effect upon the bacteria, its *p*H was determined by means of a Macbeth line-operated *p*H meter. A series of tests was also performed to determine the inhibitory effect of H-ions and OH-ions in buffer solutions of assorted *p*H in order to ascertain whether or not the inhibitory effects of the different plant extracts might be merely a reflection of their *p*H values. The buffer solutions were prepared from tablets each of which, upon being dissolved in 100 ml. of distilled water, gave a solution of specified *p*H value.[2]

Information concerning the plants reported in this paper is presented in Table 1, which shows (1) the major plant group and the family to which each plant belongs; (2) the scientific name of the plant; (3) the common names of the plant, in both English and Hawaiian; and (4) epitomes of the usual purposes for which the plant was employed, according to the references consulted in preparing the list (the specific references are cited in the table).

We can make no claim to being taxonomists and have based our presentation of the systematic relationships of these plants upon the manner in which Neal has set them forth in her recent book *In Gardens of Hawaii* (1948). In her introduction to this compendium, Miss Neal states that she has followed the system of Engler and Prantl for the flowering plants, and the arrangement of A. J. Eames for the ferns and fern allies.

The single specimen of alga collected, *Gracilaria furcellata,* was identified by Dr. Marion L. Lohman, associate professor of botany at the University of Hawaii. Most of the

[2] The tablets are produced by the Coleman Electric Company, Maywood, Ill.

TABLE 1

SCIENTIFIC AND COMMON NAMES OF THE PLANTS TESTED, THEIR SYSTEMATIC RELATIONSHIPS, AND THE MEDICINAL USES TO WHICH THEY WERE PUT

(K & A = Kaaiakamanu and Akina, 1922; Deg. = Degener, 1930; Handy = Handy, Pukui, and Livermore, 1934; Neal = Neal, 1948)

FAMILY	SCIENTIFIC NAME OF SPECIES	COMMON NAMES IN HAWAII	TRADITIONAL USES AS MATERIA MEDICA
Gracilariaceae	*Gracilaria furcellata* Mont.	seaweed; *limu manauea* (?)	sores, skin blotches, "cure for miscarriage" (K & A: 62)
Psilotaceae	*Psilotum nudum* (L.) Griseb.	upright *Psilotum; moa*	thrush, diarrhoea in infants (Deg.: 20; Neal: 7)
Gleicheniaceae	*Dicranopteris linearis* (Burm.) Underw.	false staghorn fern; *uluhe*	laxative (Deg.: 27)
Polypodiaceae	*Nephrolepis biserrata* (Sw.) Schott.	related to Boston fern; *okupukupu*	not known (listed in Handy: 44)
	Cibotium Chamissoi Kaulf.	tree fern; *hapu*	asthma, "lung troubles" (K&A: 16)
Pandanaceae	*Freycinetia arborea* Gaud.	climbing screwpine; *ieie*	general debility, thrush, high fever (K & A: 22)
	Pandanus Rockii Mart.	a screwpine, related to the *hala* of the Hawaiians	*hala* was used for general debility, constipation, "pain in chest" (K & A: 41); asthma (personal communication)
Gramineae	*Bambusa* sp.	"small-leaved bamboo"; *ohe laulii*	ulcers and scrofulous sores (K & A: 30)
	Coix lacryma-jobi L.	Job's tears; *pu oheohe*	curative charm (Neal: 74)
	Saccharum officinarum L.	sugar cane; *ko kea*	cuts and wounds, urethritis (K & A: 6, 53); adjuvant (Handy: 21); pulmonary disease (personal communication)
	Setaria palmifolia (Willd.) Stapf	palm grass	use unknown; hearsay
	Stenotaphrum secundatum (Walt.) Ktze.	buffalo grass; *akiaki, manienie mahikihiki*	sores and ulcers on skin (K & A: 10)
Cyperaceae	*Scirpus validus* Vahl.	great bulrush; *aka'akai naku, neki*	"gripping pain of the stomach or intestines, and for intestinal hemorrhages" (K & A: 10)
Palmae	*Cocos nucifera* L.	coconut; *niu*	general debility and cuts (K & A: 73); thrush (Handy: 22)
Araceae	*Alocasia macrorrhiza* (L.) Sweet	*ape keokeo*	burns, stomach ache, aphrodisiac (K & A: 17)
	Colocasia esculenta (L.) Schott.	taro; *kalo*	laxative (K & A: 17)
Commelinaceae	*Commelina diffusa* Burm. f.	day flower; *honohono, makolokolo*	"purifying the blood" (K & A: 71)
Liliaceae	*Allium fistulosum* L.	green onion; *aka'akai*	tuberculosis, colds, and venereal diseases (K & A: 10)
	Cordyline terminalis (L.) Kunth. var *Ki* (Schott.) J. G. Baker	*ti, ki, lau'i*	asthma, congestion of lungs, high fever (K & A: 50)
Dioscoreaceae	*Dioscorea alata* L.	yam; *uhi*	high fever (K & A: 37)
Musaceae	*Musa paradisiaca* L. ssp. *sapientum* (L.) Ktze. var.	banana; *mai'a*	asthma, general debility, stomach disorders (K & A: 65–68); throat infection (personal communication)

TABLE 1 *(Continued)*

FAMILY	SCIENTIFIC NAME OF SPECIES	COMMON NAMES IN HAWAII	TRADITIONAL USES AS MATERIA MEDICA
Zingiberaceae	*Alpinia purpurata* (Vieill.) K. Schum.	red ginger	use unknown; hearsay
	Hedychium coronarium Koenig	white ginger; *awapuhi keokeo*	"for foetid nostrils" (K & A: 20)
	Zingiber Zerumbet (L.) Smith	mountain ginger; *awapuhi kuahiwi*	cuts and sores (K & A: 19)
Casuarinaceae	*Casuarina equisetifolia* L.	ironwood	astringent (Neal: 247)
Piperaceae	*Peperomia membranacea* H. & A.	peperomia; *alaalawainui*	general debility, pulmonary diseases, venereal diseases, scrofulous swellings and ulcers (K & A: 13–14)
	Peperomia latifolia Miq.	peperomia; *alaalawainui*	same as above
Moraceae	*Artocarpus incisus* (Thunb.) L. f.	breadfruit; *ulu*	skin diseases and boils (K & A: 38; Handy: 31)
	Morus alba L., f. *nigrobacca* Mold.	mulberry; *kilika*	use unknown; hearsay
Urticaceae	*Touchardia latifolia* Gaud.	*olona, wauke-malulo*	"bodily ailments or weaknesses" (K & A: 71)
Santalaceae	*Santalum album* L.	Indian sandalwood; related to the *iliahi* of the Hawaiians	*iliahi* was used for sores, venereal diseases (K & A: 24; Neal: 278)
Amaranthaceae	*Amaranthus spinosus* L.	spiny amaranth; *pokai kuku*	use unknown; hearsay
Nyctaginaceae	*Mirabilis Jalapa* L.	four o'clock; *nani ahiahi*	poultices, purgatives (Neal: 288)
Batidaceae	*Batis maritima* L.	pickleweed; *akulikuli kai*	"leaves have medicinal value" (Neal: 291)
Portulacaceae	*Portulaca oleracea* L.	pigweed; *akulikuli kula, ihi-ai, lumaha'i*	general debility (K & A: 24)
Cruciferae	*Nasturtium officinale* R. Br.	water cress; *leko*	"for dry throat and cold in the head," asthma (K & A: 64); tuberculosis (personal communication)
Crassulaceae	*Bryophyllum pinnatum* (Lam.) Kurz.	air-plant	fevers (Neal: 329)
Pittosporaceae	*Pittosporum Tobira* (Thunb.) Ait.	related to the *ho'awa* of the Hawaiians	*ho'awa* was used for sores (Neal: 335); scrofula (K & A: 44)
Rosaceae	*Rubus rosaefolius* Sm.	thimbleberry	use unknown; hearsay
Leguminosae	*Acacia confusa* Merr.	Formosa koa	use unknown; chosen for its relationship to *Acacia Koa*
	Acacia Koa Gray	*koa, kahilikolo*	general debility, diseases of the skin (K & A: 46)
	Cassia Leschenaultiana DC.	cassia; *lauki*	use unknown; hearsay
	Crotalaria incana L.	rattlebox; *pikakani*	use unknown (listed in Handy: 74)
	Crotalaria mucronata Desv.	rattlebox; *pikakani*	use unknown; hearsay
	Dioclea violacea Mart.	sea bean; *mannaloa*	cuts, skin diseases, "purifying the blood" (K & A: 65)
	Leucaena glauca (L.) Benth.	false koa; *koa haole*	use unknown; hearsay
	Medicago sativa L.	alfalfa	use unknown; hearsay
	Prosopis chilensis (Mol.) Stuntz	algaroba; *keawe*	dysentery, sore throat (Neal: 363)

TABLE 1 *(Continued)*

FAMILY	SCIENTIFIC NAME OF SPECIES	COMMON NAMES IN HAWAII	TRADITIONAL USES AS MATERIA MEDICA
	Tamarindus indica L.	tamarind; *wi 'awa 'awa*	"used medicinally in India" (Neal: 366)
	Vigna marina (Burm.) Merr.	*nanea, okoleomakili*	general debility, asthma, boils and cuts (K & A: 33)
Rutaceae	*Citrus aurantifolia* (Christmann) Swingle	lime	use unknown; hearsay
	Pelea sp.	*alani*	general debility, "purifying the blood," skin diseases: "makes the skin immune to certain diseases" (K & A: 16)
Euphorbiaceae	*Aleurites moluccana* (L.) Willd.	candlenut tree; *kukui*	general debility, asthma, scrofulous sores, ulcers of skin (K & A: 56–57); diphtheria (personal communication)
	Euphorbia hirta L.	hairy spurge; *kokokahiki, akoko*	cathartic, gargle, poultice (Handy: 19); thrush (Deg.: 198)
	Euphorbia pulcherrima Willd.	poinsettia; *koko*	use unknown (listed in Handy: 39, 44)
	Euphorbia Milii Ch. des Moulins	crown-of-thorns	use unknown; hearsay
	Euphorbia Tirucalli L.	pencil plant	use unknown; hearsay
	Hura crepitans L.	sand-box tree	"leprosy and other conditions" (Neal: 451)
	Ricinus communis L.	castor bean; *koli, pa'aila*	fever (K & A: 55)
Anacardiaceae	*Mangifera indica* L.	mango; *manako*	astringent (Neal: 457)
	Schinus terebinthifolius Raddi	Christmas berry tree; *wilelaiki*	use unknown; hearsay
Sapindaceae	*Cardiospermum Halicacabum* L.	balloon vine, heartseed; *inalua, poniu*	rheumatism, digestive and pulmonary disorders (Neal: 467)
	Dodonaea viscosa L.	*aalii, kumakani*	rash and itch (K & A: 2)
Malvaceae	*Hibiscus tiliaceus* L.	*hau kae kae*	laxative (Neal: 49); congested chest, sore throat (K & A: 40)
	Malvastrum coromandelianum (L.) Garcke	false mallow	poultices (Neal: 485)
	Sida fallax Walp.	*ilima*	general debility, asthma, "fallen womb," laxative (K & A: 26; Neal: 485)
Sterculiaceae	*Waltheria americana* L.	*hialoa, uhaloa, kanakaloa*	asthma, sore throat, pulmonary complications (K & A: 37; Neal: 503; personal communication)
Guttiferae	*Calophyllum Inophyllum* L.	Alexandrian laurel; true *kamani*	use unknown (listed in Handy: 43; Neal: 513)
Passifloraceae	*Passiflora edulis* Sims f. *flavicarpa* Degener	yellow *lilikoi*	use unknown; hearsay
	Passiflora foetida L. var.	running pop, red passion fruit	use unknown; hearsay
	Passiflora sp.	green *lilikoi*	use unknown; hearsay
Caricaceae	*Carica Papaya* L.	papaya; *nikana, he'i*	skin diseases (Neal: 527); deep cuts (K & A: 43)
Cactaceae	*Opuntia megacantha* Salm-Dyck	prickly pear; *panini*	constipation (K & A: 73)

TABLE 1 *(Continued)*

FAMILY	SCIENTIFIC NAME OF SPECIES	COMMON NAMES IN HAWAII	TRADITIONAL USES AS MATERIA MEDICA
Thymeliaceae	*Wikstroemia oahuensis* (Gray) Rock	*akia*	laxative, asthma (K & A: 8); fish poison (Neal: 540; Deg.: 224–225)
Punicaceae	*Punica Granatum* L.	pomegranate; *pomaikalana*	used in Orient (Neal: 551)
Combretaceae	*Terminalia Catappa* L.	tropical almond; false *kamani*	"used medicinally" (Neal: 551)
Myrtaceae	*Eucalyptus* sp.	eucalyptus; *nuholani*	fevers, sores, pains, rheumatism (K & A: 73)
	Eugenia Cumini (L.) Druce	Java plum	use unknown; hearsay
	Eugenia malaccensis L.	mountain apple; *ohia ai*	general debility, thrush, sores, cuts (K & A: 31–32); throat infection (personal communication)
	Metrosideros macropus H. & A.	*ohia lehua, ohia hamau*	sore throat, bronchitis, consumption, wounds (Handy: 20)
	Psidium Guajava L.	guava; *kuawa*	"medicinal tea" (Neal: 556); deep cuts, sprains, diarrhoea, intestinal hemorrhages (K & A: 55)
Apocynaceae	*Nerium Oleander* L.	oleander; *oleana*	skin diseases (Neal: 611)
	Thevetia peruviana (Pers.) K. Schum.	be-still, yellow oleander	"used medicinally" (Neal: 610)
Convolvulaceae	*Ipomoea Batatas* (L.) Poir.	sweet potato; *uala*	medicinal uses (Handy: 21); asthma, constipation, "fallen womb" (K & A: 35–36)
	Ipomoea congesta R. Br.	morning glory; *koali awahia*	purgative, healing broken bones (Handy: 19; K & A: 52; Neal: 623); relief of muscular pain (personal communication)
	Ipomoea pes-caprae (L.) Sweet	beach morning glory; *pohuehue*	"good for the expectant mother" (K & A: 73)
Boraginaceae	*Messerschmidia argentea* (L. f.) Johnston	tree heliotrope; *tahinu*	use unknown; hearsay
Verbenaceae	*Lantana Camara* L.	lantana; *lakana*	use unknown; hearsay
	Stachytarpheta cayennensis (L. C. Rich.) Vahl.	vervain; *oi*	"used in tropical America" (Neal: 639)
Solanaceae	*Capsicum frutescens* L.	red pepper; *nioi*	pains in back, rheumatism, swollen feet (K & A: 72)
	Lycopersicon esculentum Mill. ssp. *Galeni* (Mill.) Luckwill	currant tomato; *ohia makanahele*	use unknown; hearsay
	Solanum nodiflorum Jacq.	black nightshade; *popolo*	disorders of respiratory tract, skin eruptions, cuts, wounds (Handy: 18; Neal: 655); trachoma (personal communication)
	Solanum sodomaeum L.	apple of Sodom; *popolo kikania*	used in Africa for skin diseases (Neal: 655)

TABLE 1 (*Continued*)

FAMILY	SCIENTIFIC NAME OF SPECIES	COMMON NAMES IN HAWAII	TRADITIONAL USES AS MATERIA MEDICA
Plantaginaceae	*Plantago lanceolata* L.	narrow-leaved plantain; *laukahi*	sores or boils (Handy: 21); general debility, constipation, boils (K & A: 58); diabetes and "to clear the system" (Neal: 695)
	Plantago major L.	broad-leaved plantain; *laukahi*	same as above
Rubiaceae	*Morinda citrifolia* L.	Indian mulberry; *noni*	broken bones, deep cuts (K & A: 73); cuts, bruises, sores, wounds (Handy: 18)
Cucurbitaceae	*Momordica Charantia* L.	bitter melon, balsam pear	used in the preparation of a Japanese remedy for skin ailments, headache, constipation (Neal: 709)
Goodeniaceae	*Scaevola frutescens* (Mill.) Krause var. *sericea* (Forst. f.) Merr.	beach naupaka; *naupaka kahakai*	"used medicinally in Malaya" (Neal: 720); cuts and skin diseases (K & A: 72)
	Scaevola Gaudichaudiana Cham.	mountain naupaka; *naupaka kuahiwi*	same as above
Compositae	*Bidens pilosa* L.	beggar tick; related to the *ko'oko'olau* of the Hawaiians	"used medicinally" (Neal: 742)
	Erigeron albidus (Willd.) Gray	related to Canada fleabane; *iliohe*	"used medicinally in Java" (Neal: 733; listed in Handy: 42)

plants were identified for us by Dr. Harold St. John, professor of botany and chairman of the Department of Botany at the University of Hawaii. We are grateful for their help and their encouraging interest in these studies. At Dr. St. John's suggestion, herbarium specimens of the plants studied were prepared by us and are preserved in the Department of Bacteriology at the University of Hawaii.

DATA AND DISCUSSION

We are well aware of the shortcomings of this approach to an appraisal of the medicinal plants found in Hawaii, if only because so many of these plants were not used primarily for their effect against bacteria: they were used as cathartics, vermifuges, emollients, astringents, analgesics, counterirritants, and other salutaries, as well as for their action in preventing infection and for treating an infection once it had begun. We know, too, that studying the effects of these plants upon bacteria *in vitro* does not test them under the conditions *in vivo* in which they were intended to be used: there are so many factors involved in the living body which might contribute important assistance to the medicinal agent when it is properly applied by the herbalist. The purists among admirers of the *kahuna's* lore will also point out that we did not use the ancient prescriptions exactly as they were applied by the *kahuna*. To this our answer must be that, in this initial stage of the investigation, we were concerned with studying the effects of the component parts of the prescriptions, hoping that later, when we had found all of the components, we could put them together to see if they are any more effective when they are used concurrently than when they are used alone.

The number of kinds of plants available

for study was limited, too. Many of those which played an important part in the *kahuna's* pharmacy were difficult to obtain even in their day, and are even harder to find now. Some of them have become extinct or inaccessible, and most of the plants grow in habitats so far removed from the laboratory that they are not conveniently available for study.

The number of species of bacteria we could use to determine the "spectrum" of activity of a plant—that is, the range of its effectiveness as an antagonistic agent for the different species of bacteria— was so limited by the time and facilities at our disposition that we could not possibly expose all of the different micro-organisms which might have assailed a susceptible Hawaiian.

Nonetheless, the determination of the antibacterial effect of extracts of the different medicinal plants offers the one feasible means for assaying them in the absence of human cases to study or of laboratory animals to experiment upon.

Before very many plants were tested it became evident that there were great variations in effectiveness of the plant extracts obtained from the different species of plants, and, indeed, often among extracts obtained from the several parts of the same plant. There was also considerable variation in effectiveness of many of the extracts against the several different test organisms.

It is difficult, then, to tabulate easily the results obtained in this study. We have finally decided to do what the Hawaiians did, and to treat each separate part of a plant as an entity of its own—if only because we found, as they did, that the different parts of the plant vary astonishingly in their pharmacological properties.

We set some arbitrary standards of efficacy, basing these standards upon the Oxford group's definition of a unit of penicillin—that amount of penicillin which gives an inhibition zone 24 mm. in diameter—and the work of Sanders *et al.* (1945) in appraising the antibacterial substances in plants collected in Indiana. Four categories were established, based upon the diameters of the zones of inhibition obtained with the plant extracts *against any one of the test organisms:*

1. Very effective: zones more than 20 mm. in diameter
2. Moderately effective: zones between 10 and 20 mm. in diameter
3. Slightly effective: zones less than 10 mm. in diameter
4. Ineffective: no apparent zone of inhibition

The summarized data of our studies are presented in Tables 2–6 and in a simple listing of the ineffective extracts (see p. 179). Table 2 presents the results of the studies with buffer solutions of different *p*H values. Tables

TABLE 2

EFFECT OF BUFFER SOLUTIONS OF DIFFERENT *p*H UPON THE TEST BACTERIA

TEST ORGANISMS	ZONES OF INHIBITION (IN MM.) ACHIEVED BY 0.2 ML. OF BUFFER SOLUTIONS		
	*p*H 3.0	*p*H 4.0	*p*H 5.0, 6.0, 8.0
Micrococcus pyogenes var. *aureus*	10	0	0
Escherichia coli	10	8	0
Pseudomonas aeruginosa	12	8	0
Salmonella typhosa	8	0	0
Salmonella montevideo	10	0	0
Salmonella schottmuelleri	12	8	0
Shigella paradysenteriae BH	13	0	0
Shigella paradysenteriae III-Z	13	0	0

3–6 are concerned with the antibacterial effects of the plant extracts and present this information: (1) the scientific name of the plant; (2) the part of the plant yielding the extract being tested; (3) the *p*H of the extract; and (4) the diameters of the zones of inhibition, measured in millimeters, developed against the different test organisms. Wherever, by intention or by accident, a particular bit of information was not obtained, a question mark (?) indicates this fact; the words "not tested" mean that the organism (usually *Ps. aeruginosa*) was not used in the testing of a particular extract; the symbol "qns" means "quantity not sufficient" to obtain a *p*H determination; the symbol "O" means no apparent zone of inhibition.

The tests showed that very acid buffer solutions (*p*H 3.0 and 4.0) are only moderately effective in their ability to inhibit growth of the test organisms, and that solutions with *p*H values ranging from 5.0 to 8.0 had no effect at all.

This is an observation that has direct bearing upon the results disclosed in this study of extracts from Hawaiian medicinal plants, for, in a number of instances—as will be seen from Tables 3 to 6—it was found that the zones of inhibition produced by the extracts were far greater than were the zones of inhibition produced by the buffer solutions having the same *p*H values as did the extracts being tested. In those extracts having a *p*H more acid than 3.0, moreover, the degree of inhibition achieved by the extracts was significantly greater than that achieved by the buffer solution of *p*H 3.0. On the other hand, as the list on page 179 shows, there were also many extracts of moderate acidity which exerted no inhibitory effect at all upon the test bacteria.

The implication here is that, in those plant extracts which are potent in their degree of inhibition of the test bacteria, it is not so much the mere *p*H of the extract that is the effective antibacterial agent, but rather the

TABLE 3
EXTRACTS WHICH EXHIBIT VERY EFFECTIVE ANTIBACTERIAL PROPERTIES
(with zone of inhibition 20 mm. or more in diameter)

NAME OF PLANT	PART OF PLANT PROVIDING EXTRACT	*p*H OF EXTRACT	DIAMETER OF ZONES OF INHIBITION (IN MM.) *M. pyogenes*	*E. coli*	*Ps. aeruginosa*
Dicranopteris linearis	leaves and stems	4.6	21	0	13
Alpinia purpurata	leaves	6.6	10	22	20
Acacia Koa	stems	5.6	20	0	0
Tamarindus indica	ripe fruit	2.4	30	30	not tested
	fruit, aqueous extract	?	25	24	not tested
	green fruit	2.5	25	26	25
Citrus aurantifolia	fruit	2.6	27	25	25
Hura crepitans	flowers	4.5	20	14	(discolored)
Passiflora edulis f. *flavicarpa*	green fruit	3.4	27	28	30
	ripe fruit	3.7	22	22	20
Passiflora foetida var.	fruit	4.2	15	32	15
Passiflora sp.	flowers	5.6	10	35	10
Punica Granatum	whole fruit*	3.5	20	20	15
	fruit-rind	3.7	22	0	13
Eugenia malaccensis	seeds	4.7	25	0	0
	bark*	5.9	20	0	not tested
	leaves*	5.4	20	0	not tested
Metrosideros macropus	stems	4.9	30	8	8
Psidium Guajava	leaves and flowers	?	20	10	not tested

* See Table 6.

TABLE 4

EXTRACTS WHICH EXHIBIT MODERATELY EFFECTIVE ANTIBACTERIAL PROPERTIES
(with zones of inhibition between 10 and 20 mm. in diameter)

NAME OF PLANT	PART OF PLANT PROVIDING EXTRACT	*p*H OF EXTRACT	DIAMETER OF ZONES OF INHIBITION (IN MM.) *M. pyogenes*	*E. coli*	*Ps. aeruginosa*
Psilotum nudum	whole plant	5.2	15	0	8
Nephrolepis biserrata	stems	5.1	12	0	0
Cibotium Chamissoi	leaflets	4.6	14	15	12
	buds (of leaves)	5.2	10	0	8
Freycinetia arborea	stems	5.8	11	0	0
Allium fistulosum	whole plant	4.3	10	8	10
Alpinia purpurata	stem	5.9	10	12	15
Artocarpus incisus	male and female flowers	6.3	0	11	not tested
Bryophyllum pinnatum	bark	5.2	0	8	10
	leaf	4.8	0	8	10
Acacia Koa	true leaves	5.5	13	0	0
	phyllodes	5.6	16	0	0
Tamarindus indica	leaves and stems	3.8	12	0	not tested
Aleurites moluccana	leaves and stems	5.8	10	0	0
	flowers	5.0	10	0	0
	leaves only	6.4	10	0	0
Euphorbia pulcherrima	floral parts	5.1	0	0	12
	leaves and stems	5.5	0	0	12
Euphorbia Milii	leaves	4.9	10	0	0
	stems	5.6	10	0	0
Euphorbia Tirucalli	stems	4.5	15	8	8
Mangifera indica	leaves	5.2	12	? (discolored)	not tested
	bark and stems	4.8	11	? (discolored)	not tested
	fruit, small, green	3.5	18	16	not tested
	fruit, half-ripe	3.2	13	15	9
Passiflora sp.	leaves and stems	6.1	12	10	0
Punica Granatum	fruit, seeds*	3.8	14	0	11
Terminalia Catappa	leaves and stems	4.8	18	0	0
Eucalyptus sp.	leaves and stems	4.8	13	0	0
Eugenia Cumini	leaves	5.0	17	12	0
	stems	5.0	15	0	0
	buds and flowers	4.5	15	0	0
Eugenia malaccensis	leaves*	3.4	12	11	11
	fruits (without seed)	4.5	14	18	0
Metrosideros macropus	leaves and buds	4.3	18	17	18
Psidium Guajava	fruit*	3.5	18	16	not tested
Ipomoea Batatas	stem	6.7	18	0	not tested
Solanum nodiflorum	green fruit	4.6	0	0	10
	ripe fruit*	4.7	0	0	18
	leaves and stems	5.8	10	10	0
Solanum sodomaeum	leaves	5.6	10	0	0
	stems	5.6	10	0	0
	fruits	5.1	10	0	0
Plantago major	whole plant*	5.5	11	10	not tested
Morinda citrifolia	ripe fruit*	4.4	15	10	15
Scaevola Gaudichaudiana	stems	5.9	16	0	0
	fruits and flowers	5.7	13	0	0
Bidens pilosa	whole plant*	5.8	15	15	12

* See Table 6.

nature of the substances which are present in the plant juices. In other words, and as herbalists and pharmaceutists long ago realized, it is the possession of chemical properties peculiar to itself that makes a plant different from its neighbors and superior to some of them for use as a medicine. The medicinal plants in Hawaii are no exception to this obvious rule. We are not able to say what substances in the tissues of the more effective of the Hawaiian plants are responsible for their efficacy.

The results of the tests with the actual extracts show that of the 101 species studied, 13 possess a considerable degree of effectiveness against the test bacteria (Table 3). Four of these plants—*koa, Acacia Koa;* mountain apple, *Eugenia malaccensis; ohia lehua, Metrosideros macropus*; and guava, *Psidium Guajava*—the Hawaiians have employed in the treatment of cuts and wounds and "skin diseases," or of bacterial infections like "diarrhoeas and dysenteries," but most of the others are plants which do not appear to have played much of a part in the treatment of conditions caused by bacteria. Most of them—*Alpinia purpurata, Tamarindus indica, Citrus aurantifolia, Hura crepitans,* the three *Passiflora* species, and *Punica Granatum*—do not seem to have been used at all by the Hawaiians, possibly because of their relatively recent introduction into Hawaii. One plant, the *uluhe, Dicranopteris linearis,* was used by the Hawaiians as a laxative, but not, as far as we know, in the treatment of conditions in which bacteria were implicated as the causative agents. All of these plants are worthy of further study to see if it is possible to obtain from any of them a useful antibacterial substance.

An even greater number of plant species is moderately effective in the action against the test bacteria (Table 4). Among these are several of the more famous and the more favored of the Hawaiian remedies: the *kukui, Aleurites moluccana*; the *popolo, Solanum nodiflorum*; the *noni, Morinda citrifolia*; the *laukahi, Plantago major*; and *Bidens pilosa,* a relative of the native "tea," *ko'oko'olau.* All of these plants had a great number of uses in Hawaiian medicine, and the *popolo* in particular has been called "ke kumu o ka lapaau o Hawaii nei"—"the foundation of Hawaiian pharmacy" (Handy *et al.,* 1934: 18). The juices of its leaves and berries were used, either alone or in combination with other ingredients, for diseases of the skin, in the treatment of cuts and wounds, in "disorders of the respiratory tract," and for "toning up the digestive tract" (Handy *et al., loc. cit.*).

Our studies showed that each of the favor-

TABLE 5
EXTRACTS WHICH EXHIBIT SLIGHTLY EFFECTIVE ANTIBACTERIAL PROPERTIES
(with zones of inhibition less than 10 mm. in diameter)

NAME OF PLANT	PART OF PLANT PROVIDING EXTRACT	*p*H OF EXTRACT	DIAMETER OF ZONES OF INHIBITION		
			M. pyogenes	*E. coli*	*Ps. aeruginosa*
Cibotium Chamissoi	stems of fronds	5.1	0	0	8
Bambusa sp.	leaves and stems	qns	7	0	0
Peperomia latifolia	whole plant	5.7	0	0	8
Pittosporum Tobira	bark*	6.2	0	0	8
	leaf*	6.1	0	0	9
Sida fallax	stems	6.2	9	0	0
Waltheria americana	water extract of leaves and stems	5.5	0	0	8
Eugenia malaccensis	stems	4.3	8	0	0
Lantana Camara	leaf	7.3	8	0	not tested

* See Table 6.

ite plants listed in Table 4 exerts some effect, at least *in vitro,* against representatives of bacterial agents of disease. Perhaps, as the users of these simples were daring enough to learn, they are even more effective when they are applied to the diseased body, when the body can contribute the weapons in its own armory to the attack upon the invading bacteria. Perhaps, too, when they are compounded with other herbs in the complex recipes which many of the *kahunas* prescribed, the total effect of the combination of ingredients is superior to the effect of each of the recipes' components.

Here is one of the simpler prescriptions, taken from the wonderfully naïve herbal of Kaaiakamanu and Akina (1922: 57):

"For scrofulous sores, bad cases of ulcer, and other bad sores where the flesh seems to rot away, the following mixture is recommended: Take the meat of eight *kukui* nuts and have it baked in *ki* leaves until thoroughly cooked. This is pounded or finely ground and then set to one side. About a tablespoonful of the breadfruit milk is then secured and mixed with the prepared *kukui* meat. In the meantime about a spoonful of the finely ground *Cyperus laevigata* fibers [*ahuawa*] and a like amount of the *lama* powder [*Maba* spp.] are being thoroughly mixed. The two mixtures are then put together and thoroughly stirred and applied by spreading it [*sic*] over the sore or sores. This is done morning and evening and as long as necessary.

"Before the treatment, however, the sore should be washed with the tea of the *Bobea* spp. bark [*ahakea*] thoroughly cooked with about a gallon of water and with four red hot stones. The bark should be pounded before boiling it in order to get its strength."

Table 5 gives the information concerning the relatively few plant extracts which were only slightly effective against the test bacteria. A few of them are extracts from parts of plants which, in others of their parts, are much more effective against the test bacteria, but most of them are examples of mediocrity in performance that would sadden the heart of a *kahuna lapaau.*

The following extracts exhibited no apparent antibacterial properties: *Gracilaria furcellata* (whole plant, 5.9[a]); *Psilotum nudum* (tea, 5.2); *Nephrolepis biserrata* (leaves, 5.3); *Freycinetia arborea* (leaves, 5.9); *Pandanus Rockii* (ripe fruit, 5.1); *Coix lacryma-jobi* (whole plant, 5.6); *Saccharum officinarum* (leaves, 5.4; stems, 5.1); *Setaria palmifolia* (whole plant, 6.0); *Stenotaphrum secundatum* (leaves, 6.1; stems and roots, 6.0); *Scirpus validus* (whole plant, 6.7); *Cocos nucifera* (milk from nut, 6.7); *Alocasia macrorrhiza* (leaves, 6.0; stems, 5.8; corms and roots, 5.8); *Colocasia esculenta* (corm, 7.0); *Commelina diffusa* (whole plant, 5.4); *Cordyline terminalis* var. *Ki* (leaves and stems, 5.8); *Dioscorea alata* (tuber, 5.7); *Musa paradisiaca* ssp. *sapientum* var. (stem, 5.7; leaf, 6.2; flower bud, 5.0); *Hedychium coronarium* (roots, 6.4; leaves and stems, 6.1; buds and flowers, 6.1); *Zingiber Zerumbet* (root, 6.0; leaves and stems, 5.8; buds and flower-stalks, 6.0); *Casuarina equisetifolia* (leaves and stems, 5.1; cones, 4.5; alcoholic extract of leaves and stems, ?); *Peperomia membranacea* (whole plant, 6.0); *Artocarpus incisus* (leaves and stems, 6.2); *Morus alba* f. *nigrobacca* (leaves and stems, 6.3); *Touchardia latifolia* (bark, 6.0; stems, 6.2; leaves, 6.8); *Santalum album* (leaves and stems, 6.0); *Amaranthus spinosus* (whole plant, 6.2); *Mirabilis Jalapa* (leaves, stems, and flowers, ?; aqueous solution of seed-powder, ?); *Batis maritima* (whole plant, 5.5); *Portulaca oleracea* (whole plant, 4.5); *Nasturtium officinale* (whole plant, 4.7); *Rubus rosaefolius* (leaves and stems, 6.4); *Acacia confusa* (leaves, stems, and flowers, 5.5); *Cassia Leschenaultiana* (whole plant, 5.8);

[a]Figures in the parentheses indicate the *p*H of the respective extracts.

Crotalaria incana (leaves and stems, 5.9; seeds and pods, 5.9); *Crotalaria mucronata* (whole plant, 6.4); *Dioclea violacea* (leaf, 5.7; seed, 6.2); *Leucaena glauca* (pods, flowers, leaves, and stems, ?); *Medicago sativa* (leaves, stems, and flowers, 5.6); *Prosopis chilensis* (leaves and stems, 5.5; pods and leaves, 5.6); *Vigna marina* (whole plant, 6.0); *Pelea* sp. (leaf, 5.7); *Aleurites moluccana* (young nuts, raw, 6.3); *Euphorbia hirta* (whole plant, 5.6); *Hura crepitans* (leaves and stems, 5.2); *Ricinus communis* (leaves, 6.0; stems, 5.4; seeds, 5.9); *Mangifera indica* (fruit, ripe, 4.7); *Schinus terebinthifolius* (leaves, 4.7; berries, 5.2); *Cardiospermum Halicacabum* (leaves and stems, 6.0; fruits, 5.7); *Dodonaea viscosa* (leaves, 5.5); *Hibiscus tiliaceus* (leaves and stems, 6.2); *Malvastrum coromandelianum* (whole plant, 5.5); *Sida fallax* (leaves, ?); *Waltheria americana* (leaves and flowers, 5.5; stems, 5.5; roots, 5.8); *Calophyllum Inophyllum* (leaves, 4.8; flowers, 4.1; fruits, 5.0); *Passiflora edulis* f. *flavicarpa* (leaves and stems, 5.8); *Passiflora foetida* var. (leaves and stems, 5.5); *Carica Papaya* (leaves, 6.1; flowers, 6.2; fruit, 5.8; seeds, 5.9); *Opuntia megacantha* (leaf-pads, 4.3); *Wikstroemia oahuensis* (leaves, 6.0; stems, 6.1); *Nerium Oleander* (leaves and stems, 5.6; flowers and pods, 5.3); *Thevetia peruviana* (flowers, 6.7; leaves, 6.0; fruits, 7.1); *Ipomoea Batatas* (leaves, 7.1); *Ipomoea congesta* (whole plant, 5.5); *Ipomoea pes-caprae* (leaves and stems, 6.1; flowers and buds, 5.9); *Messerschmidia argentea* (leaves and stems, 6.0; fruits, 6.5); *Stachytarpheta cayennensis* (leaves, 6.1; stems, 6.0); *Capsicum frutescens* (leaves and stems, 5.8; tea from pods, 6.8); *Lycopersicon esculentum* ssp. *Galeni* (leaves and stems, 5.8; fruits, 4.5); *Plantago lanceolata* (whole plant, 5.5); *Morinda citrifolia* (leaves and stems, 5.1); *Momordica Charantia* (leaves, 7.3); *Scaevola frutescens* var. *sericea* (leaves and stems, 6.2; ripe fruit, 5.5); *Scaevola Gaudichaudiana* (leaves, 5.9); *Erigeron albidus* (whole plant, 5.7).

The text listing on page 179 is significant chiefly for its length. In it are included some of the species of plants which the Hawaiians often employed to treat conditions which we now recognize as bacterial infections. Among these plants are sugar cane, *Saccharum officinarum*; buffalo grass, *Stenotaphrum secundatum; awapuhi, Zingiber Zerumbet; alaalawainui, Peperomia* spp.; *alani, Pelea* sp.; *aalii, Dodonaea viscosa; uhaloa, Waltheria americana;* the poisonous *akia, Wikstroemia oahuensis;* the deadly oleanders, *Nerium Oleander* and *Thevetia peruviana;* sweet potato and the *koali* of several kinds, *Ipomoea* spp.; chili pepper, *Capsicum frutescens; naupaka, Scaevola* spp.; and many others, but, it must be pointed out, there are also included in the list a number of species of plants which were applied by the Hawaiians to the treatment of conditions other than those caused by bacteria. It is worthy of note that, in general, the *p*H values of the extracts of these plants are significantly higher (that is, less acid) than are the *p*H values of the more effective plant extracts listed in Tables 3 and 4.

Nevertheless, this list is one of disappointments, from the bacteriologists' point of view, and reveals the price of empiricism in medicine—many failures for every success.

Table 6 is in the nature of an appendix to Tables 3 to 5. It presents the effects of extracts from 17 different plants upon the 5 strains of pathogenic intestinal bacilli used in these studies. Four of the plants were very effective in their antibacterial action and might well be studied further. Only one of these, the guava, *Psidium Guajava,* was used by the Hawaiians specifically for its curative value in "diarrhoeas and intestinal hemorrhages" (Kaaiakamanu and Akina, 1922: 55). This illustrates the ability of the Hawaiian to exploit newly introduced plants for his medicinal needs, for the guava was not brought to Hawaii until early in the nineteenth century, when Don Marin im-

TABLE 6
ACTION OF CERTAIN PLANT EXTRACTS UPON FIVE ENTERIC PATHOGENS*

ACTION	NAME OF PLANT	PART OF PLANT	*p*H OF EXTRACT	ZONE OF INHIBITION (IN MM.)				
				Salmonella typhosa	*Salmonella montevideo*	*Salmonella schottmuelleri*	*Shigella paradys.* BH	*Shigella paradys.* III-Z
VERY EFFECTIVE	*Punica Granatum*	whole fruit	3.5	20	18	27	17	12
	Eugenia malaccensis	bark	5.9	0	0	0	20	20
		leaves	5.4	0	0	0	30	35
MODERATELY EFFECTIVE	*Psidium Guajava*	fruit	3.5	20	19	18	22	30
	Morinda citrifolia	ripe fruit	4.4	23	10	12	22	20
		young fruit	5.2	10	0	0	15	15
	Momordica Charantia	leaves	7.3	8	0	0	12	12
	Bidens pilosa	whole plant	5.8	17	8	8	8	8
SLIGHTLY EFFECTIVE	*Pittosporum Tobira*	bark	6.2	10	8	0	8	8
		leaves	6.1	8	8	0	8	8
	Solanum nodiflorum	ripe fruit	6.2	8	8	8	8	8
	Plantago major	whole fruit	7.0	8	7	9	8	8

*The following extracts were found to be ineffective against the enteric pathogens: *Colocasia esculenta* (corm, 7.0); *Commelina diffusa* (whole plant, 5.4); *Dioscorea alata* (tuber, 5.7); *Musa paradisiaca* ssp. *sapientum* var. (stems, 5.7; leaves. 6.2; flower bud, 5.0); *Pelea* sp. (leaves, 5.7); *Schinus terebinthifolius* (leaves, 4.7; berries, 5.2); *Dodonaea viscosa* (leaves, 5.5); *Psidium Guajava* (leaves and flowers, ?); *Ipomoea congesta* (whole plant, 5.5); *Morinda citrifolia* (leaves and stems, 5.1).

ported it (Neal, 1948: 555). (It could not have come too soon for the dying Hawaiian race, for by this time the bloody fluxes, introduced by almost every vessel calling at Hawaii, had long since begun to take their toll of native lives, and the surviving Hawaiians must have been seeking desperately for remedies against them.)

It is possible that many of the other plants which were not tested for their action upon these enteric pathogens will possess properties antagonistic to them. A minor but interesting phenomenon is the apparent selective action of some of these plant extracts upon some of the intestinal pathogens: the action of *Eugenia malaccensis,* for example, is directed against the two *Shigella* strains only; and the young fruit of the *noni, Morinda citrifolia,* also exhibits its peculiar selectivity for the two *Shigella* strains and the typhoid bacillus.

Most of the plant extracts listed on page 179, far from inhibiting the test bacteria, markedly stimulated their growth. Many of the plant extracts which showed some degree of effectiveness against the test bacteria also stimulated the growth of the bacteria in those areas around and beyond the periphery of the zones of inhibition. This action probably can be attributed to the presence of foodstuffs and of growth-promoting factors in the extracts, even in those extracts which also possess agents which are antagonistic to the bacteria. It is also possible that, as is known to be the case with many substances, the same agent in a plant extract may be inhibitory, or even bactericidal, in high concentrations and stimulating in low concentrations.

It must be remembered, too, that the efficacy of these extracts is dependent to a considerable extent upon the diffusability of their component parts. It is, therefore, highly probable that other results might be obtained if other methods of assay were employed, or that many more of the plants might be shown to have a greater degree of effectiveness

against the bacteria if their extracts were treated in such a manner as to purify or to concentrate the antagonistic agents.

In those few instances in which subcultures were taken from the zones of inhibition, the effect of the plant extracts seemed to be a bactericidal one. This claim cannot be made for all the effective extracts inasmuch as we did not prepare subcultures from all the zones of inhibition.

It should be stated here that the studies reported in this paper are merely preliminary investigations into the effectiveness *in vitro* of extracts of plants represented in the Hawaiian pharmacopeia. They are in no sense an endorsement of the *kahuna lapaau laau's* methods or a recommendation of some of these plants for popular usage today. Neither are they to be construed as a defamation of the medical folklore of Hawaii. They are merely a search for facts, upon which some day a scientific appraisal of the Hawaiian's medicines can be based, and out of which, perhaps, a useful therapeutic may emerge.

SUMMARY

Preliminary investigations into the antibacterial properties of extracts from different portions of 101 species of plants which have been used in Hawaii for various medicinal purposes showed that extracts from 13 species possessed agents which were very effective *in vitro* in their action against test strains of *Micrococcus pyogenes* var. *aureus, Escherichia coli,* and *Pseudomonas aeruginosa.* Extracts from 30 species of plants (some of the extracts being obtained from parts of the same plants other parts of which exhibited very effective antibacterial action) possessed agents which were moderately effective. The rest were either ineffective or only slightly effective in their action. Determinations of effectiveness were made by testing extracts by the Oxford cup method developed for the assay of penicillin. Extracts were obtained by submitting freshly collected plant material to pressures of 15,000 to 20,000 pounds per square inch, achieved by means of a Carver hydraulic press.

Extracts obtained from the following plants were the most effective: *uluhe, Dicranopteris linearis*; red ginger, *Alpinia purpurata; koa, Acacia Koa;* tamarind, *Tamarindus indica*; lime, *Citrus aurantifolia*; sand-box, *Hura crepitans*; three species of passion fruit, *Passiflora edulis* f. *flavicarpa, P. foetida* var., and *Passiflora* sp.; pomegranate, *Punica Granatum*; mountain apple or *ohia ai, Eugenia malaccensis; ohia lehua, Metrosideros macropus*; and guava, *Psidium Guajava.*

Extracts of 17 of the plants were studied for their effect upon 5 strains of pathogenic enteric bacilli (*Salmonella typhosa, Sal. montevideo, Sal. schottmuelleri,* and two serological types of *Shigella paradysenteriae*). Extracts from four plants—*Punica Granatum, Eugenia malaccensis, Psidium Guajava,* and *Morinda citrifolia*—appear to possess agents which are effective against some or all of the intestinal pathogens tested.

Of the plant families studied, species of the Punicaceae, Passifloraceae, Euphorbiaceae, and Myrtaceae appear to be most effective in their antibacterial action, and invite further investigation both for themselves and for other species included in these families.

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Some Stratiomyidae (Diptera) from Okinawa and Guam

MAURICE T. JAMES[1]

THE PRESENT PAPER is based on the study of a collection of Stratiomyidae from Okinawa and from Guam and the neighboring island of Rota, and now preserved in the United States National Museum and the California Academy of Sciences.

SPECIES FROM OKINAWA

Wallacea albiseta de Meijere

Wallacea albiseta de Meijere, 1907, Tijd. v. Ent., 50: 236.

Material examined: Okinawa, June to August, 1945 (W. D. Field, F. N. Young, G. E. Bohart, C. L. Harnage), 9 females, 19 males.

This widely distributed species has been misdetermined as *W. argentea* Doleschall by Brunetti and other authors.

Oplodontha rubrithorax (Macquart)

Odontomyia rubrithorax Macquart, 1838, Diptères exotiques nouveaux ou peu connus, vol. 1, pt. 1, p. 185.

Material examined: Okinawa, July to September, 1945 (F. N. Young, W. D. Field, R. Bohart), seven males, two females.

Sargus mactans Walker

Sargus mactans Walker, 1860, Proc. Linn. Soc. London, 4: 97.

Material examined: Chizuka, Okinawa, July to September, 1945 (G. E. Bohart, C. L. Harnage), one male, two females.

Ptecticus okinawae new species

Male: Head mainly yellow, with golden pile; frontal callus whitish; occiput black, subshining, with whitish pollen toward the orbits. Antenna structurally as in *P. aurifer* (Walker), yellow, the flagellum dulled with whitish pollen; arista brownish-yellow at extreme base, otherwise black. Mesonotum, scutellum, and postscutellum brownish with bluish to violaceous reflections, paler laterally; thorax otherwise reddish-yellow, the areas adjoining the sutures paler; pile golden except a tuft of short black hairs above the base of each haltere. Halteres yellow; legs uniformly reddish-yellow, the middle and hind femora with slight bluish reflections; pile of legs yellow. Wing venation as in *aurifer*; anterior part of wing as far apicad as vein R_4 and enclosing and extending beyond the discal cell yellow; wing apex and posterior half of wing uniformly grayish and contrasting with the yellow area; veins yellow in yellow area, brownish-black in gray area. Abdomen reddish-yellow in ground color but with large, poorly defined areas taking in all but posterior and lateral margins of terga one to four and of sterna four and five, brownish-black, with bluish to violaceous reflections; pile of first five terga mostly short, black; lateral and apical margins of these terga, as well as entire venter and genital segments, with golden pile. Genitalia reddish-yellow. Length, 14 mm.

Holotype: Male; Chizuka, Okinawa; July to September, 1945 (G. E. Bohart, C. L. Harnage); California Academy of Sciences.

Related to *P. aurifer* (Walker), but easily distinguishable by the lack of contrast between the gray area of the apex and of the

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posterior half of the wing; in *aurifer*, the apex is distinctly darker and this area is sharply defined from both the anterior yellow and the posterior gray areas. In size, *aurifer* is normally larger (17 to 22 mm. in length), the upper parts lack the bluish reflections, and the fifth abdominal segment, though variable, is marked with black. I can find no structural differences; the genitalia seem to be identical.

Ptecticus australis Schiner

Ptecticus australis Schiner, 1868, Novara Reise, Diptera, p. 65.

Originally described from the Nicobar Islands, this species has been recorded from Ceylon, Siam, Malaya, and various Indian localities by Brunetti, and I have seen it from Palowan, Philippine Islands. One female and five males from Chizuka, Okinawa, July to September, 1945 (G. E. Bohart, C. L. Harnage), represent a form with the hind legs somewhat paler than in the typical form; the tibia and base of the basitarsus are brown rather than black, though these areas distinctly contrast with the yellow of the hind femur and the white of the remainder of the hind tarsus. Otherwise, I note no significant difference from Indian and Philippine specimens.

Ptecticus tenebrifer (Walker)

Sargus tenebrifer (Walker), 1849, List of the specimens of Dipterous insects in the collection of the British Museum, pt. 3, p. 517.

This common Oriental and southeastern Palaearctic species is represented by a long series of males and females from Chizuka, Okinawa.

SPECIES FROM GUAM AND ROTA

Paracechorismenus guamae new species

Female: Head shining black. Vertex two-fifths head width, narrowing to the nearly parallel-sided front; front at narrowest equal to distance from anterior ocellus to the antennal insertion. Face with a few whitish hairs and with conspicuous whitish-tomentose orbits. Head profile essentially as in *intermedius* Kertész, except that the ocellar triangle is not quite so prominent. Antennae yellow, the flagellum above and the arista brownish-black; arista 1.65 length of rest of antenna. Proboscis yellow. Measurements of holotype in micrometer units (85 = 1 mm.): Width of head, 50; of vertex, 20; of front at narrowest part, 13; front, anterior ocellus to antennal insertion, 13; length of antenna excluding arista, 12; of arista, 20.

Thorax black, subshining; mesonotum and scutellum with conspicuous, rather dense, golden tomentum; posterior area of mesopleuron with similar yellow tomentum. Legs uniformly yellow, at most slightly darkened toward apices of tarsi. Halteres yellow. Wing venation typical; wings slightly clouded; heavy veins brown; veins inclosing discal cell, except at base, and those radiating from it, weak and unpigmented.

Abdomen black; pile mostly black, inconspicuous, that on fifth tergum and laterally on third and fourth terga somewhat longer and yellowish. Ovipositor yellow.

Length, 1.75 to 2.5 mm., mostly about 2 mm.

Male: Front narrower than in the female, at narrowest 0.18 to 0.20 head width and 0.65 to 0.70 distance from anterior ocellus to antennal insertion. Tomentum of mesonotum and scutellum longer but more scattered than in the female, tending more to whitish but with golden tomentum definitely intermixed and usually predominating. Genitalia yellow. Otherwise, as described for the female.

Holotype: Female, Guam, January 12, 1938 (R. G. Oakley); resting on *Ochrosia* fruits; Guam no. 1206; Lot no. 38-14973; U. S. National Museum type no. 59339. *Allotype:* Male, Point Oca, Guam, May,

1945 (G. E. Bohart, J. L. Gressitt). *Paratypes:* Seventeen females, fourteen males, same data as holotype; seven females, five males, same data as allotype; one male, one female, Point Oca, Guam, December 20, 1945 (Gressitt); one male, Asan, Guam, December 16, 1945 (Gressitt); two females, Point Oca, near Agana, Guam, May 27, 1945 (Gressitt), at lights; one female, Point Ritidian, Guam, June 28, 1945 (Bohart & Gressitt); two females, one male, Namru 2, Guam, May 7, 1945 (Gressitt).

In Kertész' key (Mus. Nat. Hungarici Ann. 14: p. 163, 1916), this species does not run past the first couplet, since the antennal flagellum is distinctly darkened above, but the arista is much longer than the rest of the antenna and the legs are almost unicolorous. The relationship is probably closest to *P. intermedius* Kertész, from Formosa, but in that species the antenna is wholly yellow, the femora are darkened on the apical third, and the mesonotal pile, anteriorly and on the swellings behind the suture, is blackish.

Wallacea albiseta de Meijere

Wallacea albiseta de Meijere, 1907, Tijd. v. Ent., 50: 236.

Material examined: Point Oca, Guam, May, 1945 (G. E. Bohart, J. L. Gressitt), two females, one male.

Cephalochrysa infuscata new species

Female: Head about 1.65 times as wide as high. Front at upper corner of eyes about one-third head width, narrowing gradually to the face, which is nearly parallel-sided on its lower part; front metallic bluish with lavender reflections, finely punctured and with fine pale hairs arising from the punctures, except along the narrow median line where it is slightly raised and glabrous, and more particularly at the anterior extremity of this line, where the glabrous areas are expanded into an inverted V; frontal callus entire, forming a transverse band which is biarcuate above, as a result of the V-shaped glabrous area; the callus whitish above, brownish below as it merges into the brownish-black of the face. Occipital orbits broad above, blue with lavender reflections and with punctures as on the front, becoming narrow and blackish below. Comparative measurements in micrometer units (30 = 1 mm.), based on holotype: Head width, 69; head height, 42; width of front, upper angle of eyes, 23; width of front, upper margin of callus, 20; width of face, 15; maximum width of occipital orbit, 9. Occiput black, with bluish reflections above. Antennae reddish-yellow; proboscis pale yellow.

Mesonotum and scutellum chiefly metallic blue, with violet reflections and with short, appressed pale pile; humeri and notopleural margin yellow, however, and postalar calli and apex of scutellum reddish-yellow, the postalar calli with black hair. Postscutellum and upper pleural areas largely metallic blue; lower pleural areas largely black but becoming yellowish in irregular and variable areas on the pteropleura and sternopleura.

Coxae, femora, hind tibia, upper surface of hind tarsus, and basal half of front and middle tibiae, especially above, blackish; all these segments usually paler basally and apically; legs otherwise yellow or yellowish. Wings infuscated, especially through the discal cell and thence along the anterior part of the apical half of the wing, the stigma the darkest; veins blackish.

Abdomen distinctly broader than the head or thorax, metallic green to blue above, with violet or purple reflections, especially on the sides or ventrally.

Length, 6–7.5 mm.; of holotype, 7 mm.

Male: Eyes, as usual, broadly contiguous. Legs more extensively pale than in the female but with the middle and hind femora, the basal half of the middle and hind tibiae, and the hind tarsi, particularly above, blackish. Wings infuscated as in the female. Ab-

domen distinctly narrower than head; pile more prominent, particularly anteriorly; venter with an extensive yellow median area on segments one to three. Genitalia yellow.

Holotype: Female, Guam, on *Ochrosia* fruit, July 25, 1938 (R. G. Oakley); Guam no. 1205; Lot no. 38-14972; U. S. National Museum type no. 59338. *Allotype:* Male, same data. *Paratypes:* One male, five females, same data; one female, Guam, December, 1945 (R. M. Bohart); one male, one female, Point Oca, Guam, June 6 and 14, 1945 (G. E. Bohart, J. L. Gressitt), at light; one female, Mt. Santa Rosa, Guam, May 16, 1945; one female, native forest near Sabana, Rota Island, 1,200 ft., June 19, 1946 (H. K. Townes).

The infuscated wings, the darkened legs, and, in particular, the infuscated hind tarsi, and the V-shaped glabrous area on the front of the female will readily distinguish this species from all others known to me. The female of *Cephalochrysa hovas* (Bigot), the genotype, has the front more coarsely punctured except on a raised area next to the median suture; this area is broad and prominent, however, and does not expand below as in *infuscata. C. hovas* has been recorded from Hawaii, but the determination may be erroneous. No raised glabrous area occurs on the front of the other Oriental species, *C. chrysidiformis* (Lind.), *C. maxima* (de Meij.) and its variety *demeijerei* (Lind.), or *C. stenogaster* James, or in any of the known American species.

The Zonation of Marine Algae at Piha, New Zealand, in Relation to the Tidal Factor[1] (Studies in Inter-tidal Zonation 2)[2]

W. A. BEVERIDGE AND V. J. CHAPMAN[3]

INTRODUCTION

THIS PAPER forms part of an inquiry into the operation of tidal factors in determining littoral zonation, and provides a comparison with work performed on the east coast of the Auckland Province (unpublished). There is still considerable confusion concerning the terminology that should be used in these ecological investigations. One of us (Chapman, 1947) has suggested that the time is now ripe for the application of ecological terms in the sense used by land workers. This viewpoint has been contested recently by Womersley (1947) but on grounds that scarcely seem adequate. In view of this confusion, however, it is still desirable to define the terms used, and in the present investigation they are as follows:

The *littoral* region is regarded as all that part of the shore between highest wash and the lowest level of spring tides. This definition is also adopted by Oliver (1923) and by Cranwell and Moore (1938).

Formation is a unit of vegetation formed by the habitat and expressed by distinctive life forms (Tansley, 1944), e.g., the Laminarian formation of Europe and the giant kelp formation of the north Pacific. (Owing to the small area studied formations have not been considered in this paper.)

Association is the largest unit of the plant formation dominated by more than one species and with at least some subordinate species, the dominants having the same ecological requirements.

Consociation is a community characterised by a single major dominant.

Society is a subordinate community *within* an association or consociation and characterised by a locally dominant subsidiary species.

Belt (*zone* of some authors) is a horizontally extended association which may be continuous round the coast, or which may be interrupted by another community, the presence of which depends on slightly different local conditions.

Aspect society is a seasonal community locally dominant.

Clan is a small aggregation of subordinate species.

Fasciation is a modification of the association in which a secondary species becomes a dominant or co-dominant.

Exposure can mean one of two things—exposure to the air during low tide periods or exposure to strong wave action. These two different types of exposure will be designated in the text by the terms *air* and *wave* exposure, respectively.

In this paper the viewpoint is adopted that the biome of the rocky sea shore represents a *physiographic climax*, since it is dependent upon the tide rather than upon the climate.

LOCALITY

Piha is situated about 7 miles north of the Manukau Heads on the west coast of New Zealand, where there is exposure to the waves

[1] This paper is a résumé of work carried out by the first author for a Master of Science degree at Auckland University College, Auckland, and has been prepared for publication by the second author.

[2] For Studies in Inter-tidal Zonation 1, see *Pacific Science* 4(1): 63–68, 1950.

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FIG. 1. View of Camel Rock, Piha, from the north. The gap is behind and to the left. The wave-cut platform at the base of the rock is clearly visible.

FIG. 2. Mouth of the gap, south of Camel Rock. Note the sharp upper limit to the algal zonation, most of which is *Durvillea*.

created by the full force of the prevailing westerly winds that blow over the Tasman Sea.

Observations were carried out mainly on Lion Rock and at the "Gap" behind Camel Rock. The former is an isolated rock 330 feet high and has a broad wave platform at about storm height. The sides of this platform slope steeply down to low water mark at most points. The second area is formed by a large off-shore rock (Camel Rock) with a narrow channel between it and the mainland; through this the sea surges with great force. There is also a tunnel through the northern end of Camel Rock in an east-west direction. (Fig. 1.)

Geologically the rocks belong to the Manukau Breccia series and consist of andesitic fragmental beds with numerous intrusive dykes and minor interbedded flows. There is no variation in the area studied.

CLIMATE

The climate is mild and equable with prevailing westerly winds, but the open coast is often exposed to strong gales which send the waves to great heights against the vertical cliffs. The sea is seldom calm and there is normally a strong surf, and even on the quietest day a considerable swell is present.

The mean annual precipitation is about 44.73 inches and the mean annual amount of sunshine, 1,914 hours. The average annual air temperature range is 26° C. with a daily shade range of about 7.0° C. The maximum shade temperature is 32.8° C. and the minimum — 0.5° C.

LITTORAL COMMUNITIES

These are described more or less from high water mark downwards.

1. **Lichina pygmaea–Melaraphe association**

   Range: upper limit of spray to M.H.W.S.[4]

   Lichina pygmaea (d)[4]
   Melaraphe oliveri (d)
   Melaraphe cincta (d)
   Entophysalis deusta (l)
   various limpets

In positions of maximum wave exposure this association may reach great heights. It is usually absent from crevices and other strongly shaded places. Of the two gastropods *M. oliveri* has the wider range since it may descend to M.H.W.N. whereas *M. cincta* occurs in the lower part of this association and in the narrow band formed by the next community.

2. **Bostrychia arbuscula consociation**

   Range: wash of M.H.W.S. to M.H.W.N.

   Bostrychia arbuscula (d)
   Rhizoclonium riparium (lf)
   Lophosiphonia macra (lf)
   Caloglossa leprieurii (lf)
   Melaraphe oliveri (f)
   Melaraphe cincta (f)
   Entophysalis deusta (seasonal)
   Enteromorpha ramulosa (seasonal)

The dominant species occurs on shady exposed rock faces in a permanently juvenile and sterile prostrate form; the adult, dark red, fertile form is to be found in moist and dark crevices.

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[4] The following abbreviations are used throughout this discussion:
E.H.W.S. = Extreme high water spring tides.
M.H.W.S. = Mean high water spring tides.
M.H.W.N. = Mean high water neap tides.
E.(L).H.W.N. = Extreme (lowest) high water mark neap tides.
M.S.L. = Mean sea level.
E.(H).L.W.N. = Extreme (highest) low water mark neap tides.
M.L.W.N. = Mean low water neap tides.
M.L.W.S. = Mean low water spring tides.
E.L.W.S. = Extreme low water spring tides.
d = dominant
a = abundant
f = frequent
o = occasional
r = rare
l = local

The consociation attains its best development amidst boulders at the back of the rock platform or in more sheltered places. *Bostrychia* does not appear able to withstand direct strong wave action. In general this belt occurs below the *Lichina* but above the main development of the barnacle zone.

Under conditions of extreme shade *Bostrychia* is replaced by *Rhizoclonium riparium* above and *Lophosiphonia macra* below. Where the shade is rather less intense *Caloglossa leprieurii* is a common associate. *Entophysalis deusta* occurs on sunny faces in summer and *Enteromorpha ramulosa* in winter.

3. **Chamaesipho association**
Range: M.H.W.S. to M.S.L.
Chamaesipho columna (d)
Chamaesipho brunnea (d)
Porphyra columbina (f–ld)
Modiolus neozelanicus (f)
Elminius plicatus (f)
Centroceras clavulatum

The configuration of the rock is important in relation to the upward extension of this association. Where the wave platform is bounded by vertical walls the association occurs up to the edge, but where the rock is sloping the surge of the waves elevates the upper limit considerably. *Chamaesipho columna* is most abundant from M.H.W.N. upwards; below it enters into competition with *Modiolus* and *Elminius*. *Porphyra columbina* apparently exists in two forms in this association. The first, which is usually small, tufted, and light green, occupies a belt from H.W.N. to H.W.S., being most abundant in sheltered and sunny areas. From H.W.N. to L.W.N. there is a larger, more flaccid, olive-red form, which, however, grades into the other form where shading occurs. The two forms may therefore represent sun and shade types.

4. **Modiolus–Chamaesipho columna association**
Range: M.H.W.N. to M.L.W.N.
Chamaesipho columna (d)
Modiolus neozelanicus (d)
Elminius plicatus (f–la)
Centroceras clavulatum (spring and summer)
Gelidium pusillum (o)
Apophloea sinclairii (o)
Chaetangium corneum (o)
Lophosiphonia macra (r)

The composition of this association varies, depending on wave action. One may therefore recognise two fasciations. The principal difference is in the greater abundance of *Elminius plicatus* under conditions of moderate wave action, whereas where there is strong wave action this species is restricted to crevices and sheltered areas. In places the *Modiolus* forms a close cover; under these circumstances it appears to be antagonistic to other animals and to plants. Only a few algae appear capable of attaching themselves to the mollusk.

Although this association is here regarded as distinct from the preceding association it must be recognised that some workers might prefer to regard it as a fasciation of the *Chamaesipho* association. It does differ however in the co-dominance of the *Modiolus*, the greater abundance of the *Elminius* under certain circumstances, and in the levels it occupies. It is for these reasons that it is here treated as a separate association.

5. **Vermilia–Hermella association**
Range: M.S.L. to M.L.W.N.
Vermilia carinifera (d)
Hermella spinulosa (d)
Modiolus neozelanicus (o)
Chamaesipho columna (o)
Gigartina alveata (o)
Gelidium caulacantheum (o)
Centroceras clavulatum (spring and summer)
Pleonosporum hirtum (o)
Caulacanthus spinellus (f)

This is an association which occurs constantly in all areas except where there is very strong wave action, and which is characterised by a distinctly restricted vertical range (about 18 inches). Both the dominants are important because they eliminate larger algae that otherwise might be present.

6. **Gigartina alveata consociation** (Fig. 3)
   Range: M.S.L. to M.L.W.N.
   Gigartina alveata (d)
   Modiolus neozelanicus (lf)
   Chamaesipho columna (f)
   Gelidium caulacantheum (la)
   Pleonosporum hirtum (summer)
   Scytothamnus australis (o)

The consociation forms a compact belt in those places where there is neither strong wave action nor extreme shelter. It always occurs above *Pachymenia himantophora* when both are present. On boulders at the head of gullies the community tends to be closed so that there are very few, if any, associated algae. In wave-exposed situations bleached and stunted specimens of *Gigartina* are scattered sparsely over the rocks.

7. **Pachymenia himantophora consociation** (Fig. 4)
   Range: E.(H).L.W.N. to about 12–18 inches below.
   Pachymenia himantophora (d)
   Lophurella caespitosa (o)
   Champia novae-zelandiae
   Gelidium caulacantheum (o)

The consociation is absent in the more sheltered localities of the open coast, and appears to reach its maximum development in gullies where the plants are exposed to heavy surge as distinct from breaking waves. On the open coast it occurs on the shoreward side of rocks with *Durvillea* at the same level on the seaward side.

8. **Gigartina marginifera consociation** (Fig. 4)
   Range: M.L.W.S. upwards for 6–9 inches.
   Gigartina marginifera (d)
   Stenogramme interrupta (o)
   Champia novae-zelandiae (o)
   Carpophyllum maschalocarpus (l)

The consociation occurs below the *Pachy-*

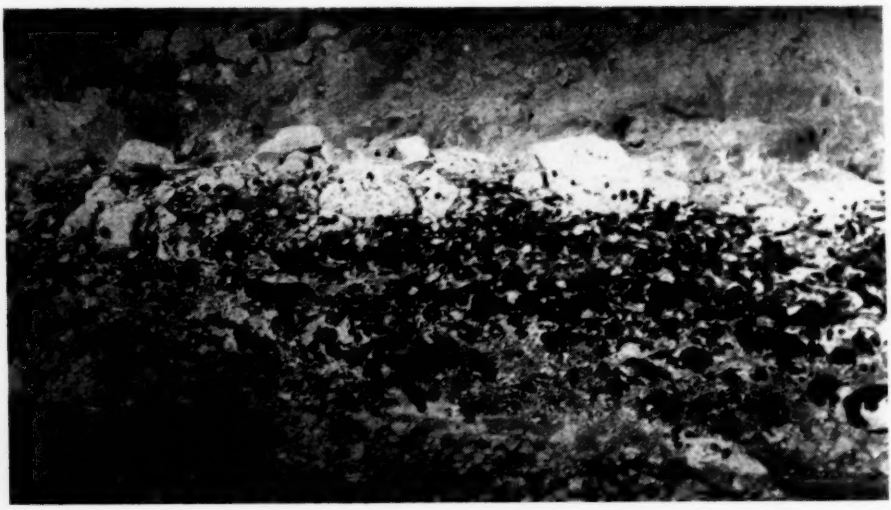

FIG. 3. A view of *Gigartina alveata* consociation with *Modiolus neozelanicus*.

FIG. 4. Algal zonation in a gully to the west of Lion Rock. At the top there is a well-marked zone of *Gigartina alveata*, below a belt of *Pachymenia himantophora* and below that *Gigartina marginifera*.

menia, flourishing especially on the flat tops of boulders in strong surge.

9. **Durvillea–Mytilus association**
Range: E.(H).L.W.N. to E.L.W.S.
Durvillea antarctica (d)
Mytilus canaliculus (d)
Gigartina marginifera (1).

The association occurs in the form of consociations dominated either by *Durvillea* or by *Mytilus*, because the two species appear to be antagonistic to each other. The upper limit of the *Durvillea* is clearly defined but the lower plants seem to thin out gradually with decreasing power of the surf. The species is essentially surf loving, and in this respect is like *Postelsia* of California. The *Mytilus* consociation is better developed in the more sheltered areas.

10. **Mytilus–attached algae association**
Range: M.L.W N. to M.L.W.S.
Mytilus canaliculus (d)
Porphyra columbina (d)
Ulva rigida (d)
Ulva linza (d)
Scytothamnus australis (d)
Gigartina atropurpurea (d)
Gigartina alveata (o)
Splachnidium rugosum (o)
Laurencia sp. (o)
Corallina sp. (o)
Centroceras clavulatum (o)
Glossophora kunthii (o)

The association is found on the shallowing floors of small caves, on flat shelves, and on boulders in moderately sheltered areas. The attached algae form colonies on the *Mytilus*, though both *Ulva* and *Porphyra* are capable of colonising the bare rock.

11. **Gigartina association**
Range: M.L.W.N. to M.L.W.S.
Gigartina atropurpurea (d)
Gigartina marginifera (d)
Mytilus canaliculus (o)
Ulva rigida (la)
Laurencia gracilis (f)
Champia novae-zelandiae
Corallina spp. (l)
Plocamium spp. (l)

The association occurs in moderately sheltered areas, *G. marginifera* tending to dominate seaward and *G. atropurpurea* shoreward. Shifting sand constantly buries parts of the association temporarily and removes the plants by scour. On re-exposure to air *Ulva* quickly recolonises the area but is replaced later by the dominants.

LOCAL COMMUNITIES OF THE MID-LITTORAL

12. **Nemastoma oligarthra society**
Range: M.H.W.N. to M.S.L.

The *Nemastoma* society was noted but once in a large gully. It disappeared in winter.

13. **Splachnidium rugosum society**
Range: M.S.L. to L.W.N.

A seasonal community that disappears in winter.

14. **Cladhymenia oblongifolia–Schizymenia sp. association**
Range: M.L.W.S. to E.L.W.S.

The association occupies the sublittoral where there is a shallowing shore and a moderate surf. It is to be found from spring to autumn and it reaches its maximum development in summer. *Champia novae-zelandiae* and *Stenogramme interrupta* are common associates.

15. **Vidalia–Melanthalia–Pterocladia lucida association**
Range: M.L.W.S. to sublittoral.

An association that occurs in long gullies below the *Pachymenia* belt. *Vidalia colensoi* is the dominant near the mouth but it is replaced by *Melanthalia abscissa* and *Pterocladia* near the head.

16. **Brackish water community**

Enteromorpha ramulosa
Enteromorpha bulbosa
Enteromorpha flexuosa
Enteromorpha nana
Bangia fusco-purpurea
Calothrix sp.
Rhizoclonium riparium

The composition of this community varies from place to place.

17. **Seasonal communities**

Scytosiphon lomentarius forms an aspect society at L.W.N. during spring but the plants are very small. *Colpomenia sinuosa,* together with *Myriogloia lindaueri,* is also abundant in spring and early summer. *Ilea (Phyllitis) fascia* is another casual occurring around L.W.N. during winter and spring.

Stephenson (1939) in his work on the zonation of South African shores distinguished three principal zones in the intertidal region: (a) *Littorina* zone; (b) balanoid zone; (c) sublittoral fringe.

It seems that this concept can be well applied to the zonation at Piha. *Melaraphe* is closely allied to *Littorina* and the balanoid zone is well represented by the species of *Chamaesipho* and *Elminius.* The sublittoral fringe can be regarded as extending from M.L.W.S. to E.L.W.S. and is occupied by the *Vidalia–Melanthalia–Pterocladia, Cladhymenia–Schizymenia, Durvillea–Mytilus,* and *Gigartina* associations according to the nature and degree of wave action.

TIDAL MEASUREMENTS AND PROCEDURE

As no tidal data were available for Piha it was necessary to erect a tide pole and to take a series of readings at high and low water. The tide pole was erected near Camel Rock in a sheltered area with its foundation at approximately E.L.W.S.T. Owing to the surf and swell, readings were restricted to calm days. When the Piha scale had been correlated with the data of the Auckland Harbour Board (A.H.B.) charts, the complete records of the Auckland tides could be used to calculate the tidal phenomena at different levels, especially those that appeared to be highly significant in respect of zonation.

The correlation data showed that on an average both high and low water records at Piha on the arbitrary tide pole scale were 0.98 (= 1 foot) foot below the corresponding levels at Auckland (A.H.B. datum). This indicates also that the tidal range at Piha is approximately the same as that at Auckland (10 feet at average spring tides).

The various fundamental tide levels were calculated using the actual Auckland marigrams for 1945. M.H.S.W., M.L.W.S., M.H.W.N., and M.L.W.N. were obtained by averaging the highest and lowest tides, respectively. The means of the equinoctial high and low spring tides gave E.H.W.S.T. and E.L.W.S.T., respectively. Similarly the figures

for E.(L).H.W.N.T. and E.(H).L.W.N.T. are obtained by calculating the means of the extreme neap tides, i.e., those with the smallest range.

	A.H.B. datum (feet)
E.H.W.S.T.	11.94
M.H.W.S.T.	11.34
M.H.W.	10.30
M.H.W.N.	9.26
E.(L).H.W.N.	8.79
M.S.L.	6.22
E.(H).L.W.N.	3.82
M.L.W.N.	3.24
M.L.W.	2.14
M.L.W.S.	1.03
E.L.W.S.	0.44

ANALYSIS OF THE TIDAL FACTOR

The tidal factor may be considered under three heads:

1. Hours of submergence and air exposure.
2. Periods of continuous air exposure or submergence.
3. Number of submergences and air exposures.

In most cases it is probable that it is a combination of factors that renders a certain level critical insofar as zonation is concerned. In respect to air exposure, the principal effect is the degree of desiccation (in its widest sense) to which the species are subjected. In the case of submergence the amount of incident light becomes important. Also to be considered is the operation of these factors at different periods in the life of the individual plants.

Level and percentage of annual air exposure (Fig. 5)

In most cases where tidal factors limit the distribution of a species, the limitation will be due not so much to a gradual change in conditions but to a more or less sudden variation in some factor. In Fig. 5 such changes occur at the 1-, 2-, 4-, 10-, and 11-foot levels. A gradual change may, however, be equally important; thus the amount of exposure is trebled between + 2 and + 3 feet. The increase at this level may be far more important than a similar increase at + 9 to 10 feet.

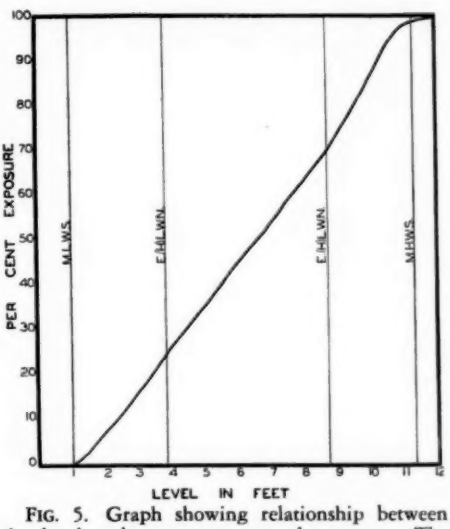

FIG. 5. Graph showing relationship between the level and percentage annual exposure. The major tide levels are also included.

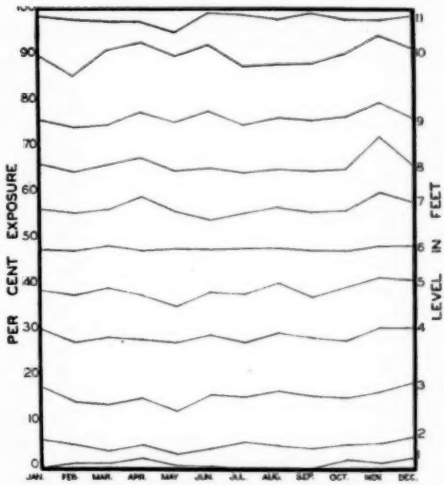

FIG. 6. The relationship between level and percentage monthly exposure.

Level and percentage of air exposure per month (Fig. 6)

It will be noted that between + 7 and + 10 feet there is an increase in air exposure in spring and autumn, this rise being most marked at the 10-foot level.

Level and continuous air exposure and submergence

This factor may operate either through the total period to which an organism is exposed or through the occurrence of an extensive period at a critical stage in development. Significant changes in the length of the maximum periods occur at + 3 feet and + 10 feet. There is also a slight increase in the total air exposure above the 11-foot level and an increase in total submergence at + 3 feet.

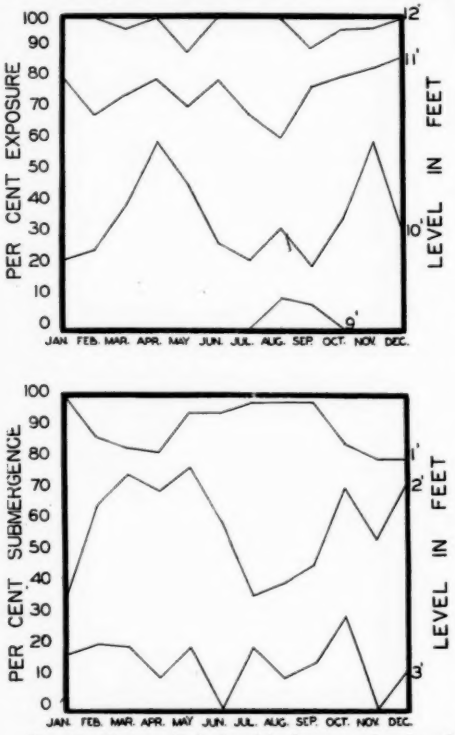

FIG. 7. *Upper.* Relationship between level and percentage continuous (non-tidal) exposure per month. *Lower.* Relationship between level and percentage continuous (non-tidal) submergence per month.

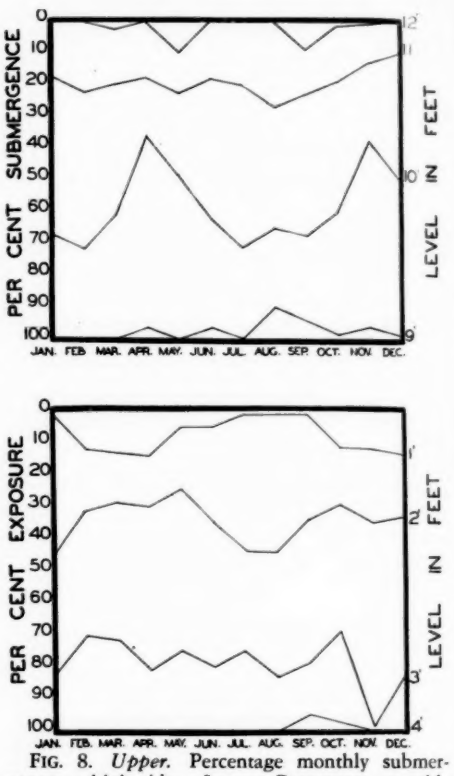

FIG. 8. *Upper.* Percentage monthly submergence at high tides. *Lower.* Percentage monthly exposure at low tides.

Level and percentage of continuous air exposure and submergence per month (Fig. 7)

There are significant changes in continuous air exposure at both the 9- and 10- foot levels. The short periods of continuous air exposure occurring in August and September at the 9-foot level may also be important in determining the upper limits of some of the more sensitive species. At the 2-foot level long submergences occur from February to May but toward winter there is a rapid decrease in length of submergence which may be of significance.

Percentage of monthly submergences and exposures (Fig. 8)

From the data given here it may be con-

cluded that species requiring a wetting each day will not grow above the 9-foot level. It will be seen too that the percentage of air exposure increases rapidly between + 2 and + 3 feet. Further, there is a significant decrease in the percentage of submergence between 9 and 11 feet.

An additional factor, that of tidal flow, which has been studied by Elmhirst (1933) and David (ms.), may exert a certain effect around E.(L).H.W.N. and E.(H).L.W.N. This effect is related to regular variations in rate of tidal flow during ebb and flood. Thus from either high or low water the tide runs 7 per cent of its height in the first hour, 18 per cent in the second hour, 25 per cent during each of the third and fourth hours, 18 and 7 per cent during the fifth and sixth hours, respectively.

RELATION OF SPECIES TO TIDE LEVELS

A levelling survey was carried out to determine the upper and lower limits of the more important algal and animal species. Only the optimum range of a species was measured, stragglers being excluded, and wherever possible levels were obtained that would give a direct expression of the tidal influence. Additional readings were also taken in places where one of the environmental factors brought about a local change in the normal level, either raising the upper limit or depressing the lower limit. The results of the levelling survey are incorporated in a series of diagrams for the different areas where the range (obtained by taking the mean of several levels) has been plotted against tide level.

In a few cases the lower limits of species growing well down on the shore are not known with certainty; this is because the sea is seldom calm at Piha and it is therefore difficult to obtain levels at low water. In these cases observation has had to supplement actual readings. Thus the levels of species growing in the vicinity of the tide pole were compiled from observations made while watching the tide pole. One may also say that up-

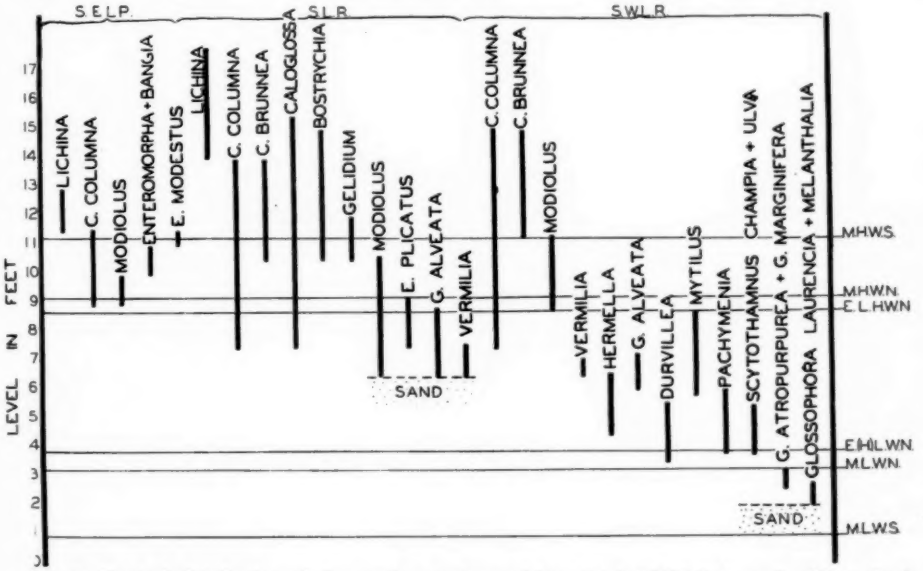

FIG. 9. Vertical distribution of the species southeast of Lion Rock (S.E.L.R.), south of Lion Rock (S.L.R.), southwest of Lion Rock (S.W.L.R.).

per limits of higher species are fairly definite but the lower limits are less pronounced unless there is severe competition.

There is also the problem of thallus length. Thus the long thalli of *Pachymenia* hang down well below the holdfast. Since, however, the sporeling phase is probably the most critical period in the life history of an alga, it is the levels delimited by the holdfasts which should be significant.

If the diagrams (Figs. 9–12) for the various areas are examined it will be seen that two major points are emphasized:

1. The zonation changes with degree and manner of wave action.
2. With increasing exposure to wave action the levels of some species are raised, those higher on the shore being more affected than those lower down.[5] At high levels the upper limit of a species is often elevated more than the lower. Thus in Figure 13 the lower limit of *Lichina* is raised by some 4 feet. In areas with maximum wave action *Lichina* and *Melaraphe* may rise at least 40 feet higher than normal.

In other species, e.g., *Chamaesipho* spp., the lower limit may remain unaffected whereas the upper limit is raised many feet by wave exposure. By contrast, *Vermilia* and *Hermella*, found in more sheltered areas, are apparently independent of wave action.

In the diagrams it will be noted that Lion Rock provides a series of habitats characterized by increasing exposure to wave action and depth of water. The diagrams show that in the different areas most species retain the same relative positions wherever they occur. *Vermilia* and *Hermella* are exceptions because they retain their positions relative to the absolute levels.

Finally, using these diagrams as a basis, an attempt was made to summarize the levelling data after making an allowance for the influence of wave action. The result is depicted in Figure 14. Since each species is affected differently by wave action, each requires a

[5] The height to which breaking waves raise the uppermost tide mark above its predicted or recorded level is referred to as the splash zone.

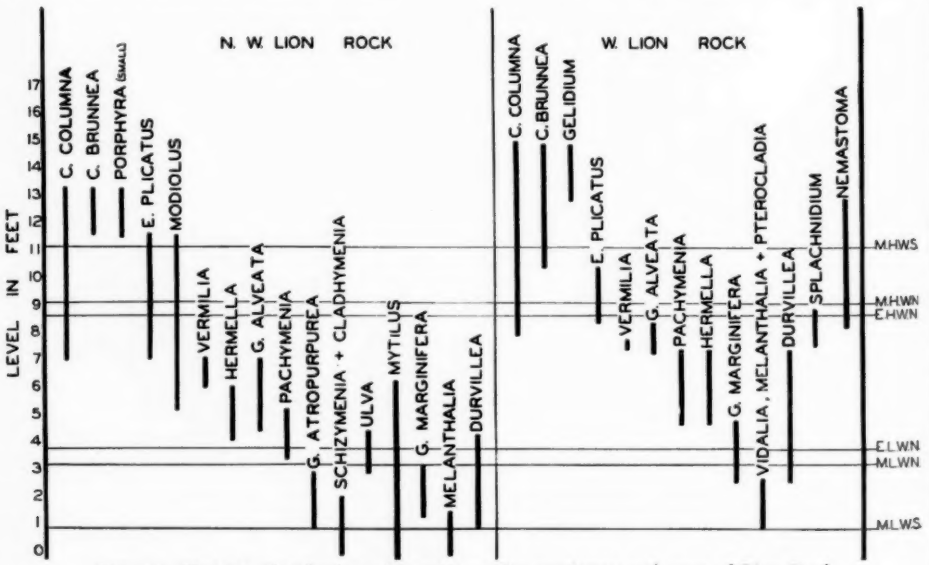

FIG. 10. Vertical distribution of species on the northwest and west of Lion Rock.

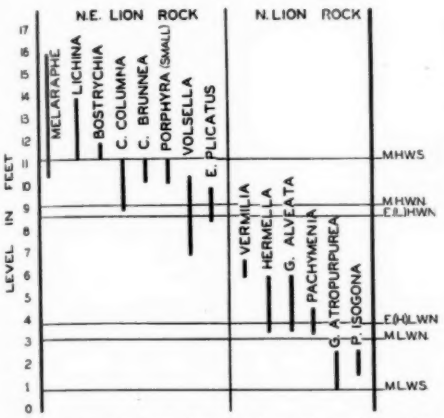

FIG. 11. Vertical distribution of species of the northeast and north of Lion Rock.

different adjustment. The chief guide used in making this adjustment was the level of the species in the most sheltered habitats. It must, however, be emphasised that owing to the great difficulties involved this attempt at allowing for wave action can only be a first approximation. From a study of this diagram it may be concluded that the most marked critical levels (i.e., levels where a number of species reach their upper or lower limit) are as follows:

	Upper limits	Lower limits	Total
11 feet—M.H.W.S. . .	6	3	9
Between 8.5 and 9.5 feet	3	3	6
4 feet—E.(H).L.W.N. .	5	2	7
3 feet—M.L.W.N. . .	5	1	6
2.3 feet	4	3	7
1.4 feet—M.L.W.S. . .	5	4	9

It will be seen that there are nine upper or lower limits between 11 feet and M.H.W.S. so that this, together with 1.4 feet, is one of the more distinctive levels. Reference to Fig-

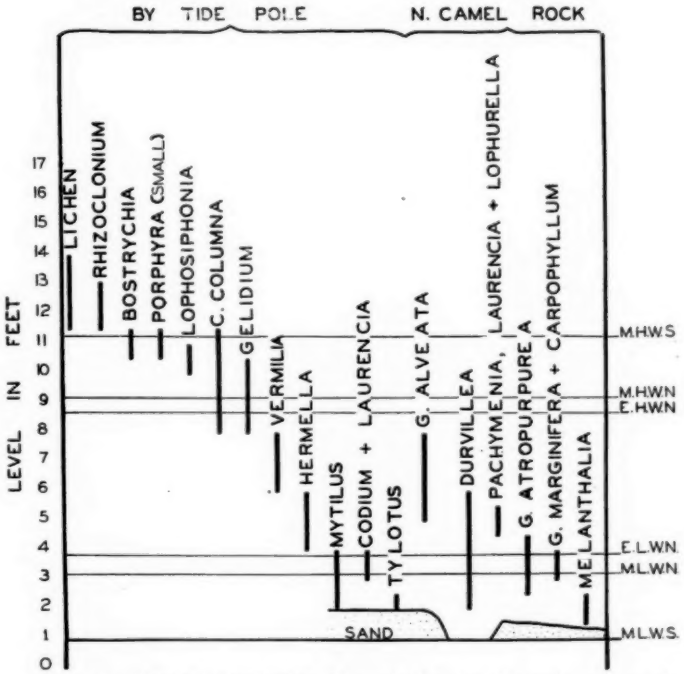

FIG. 12. Vertical distribution of species by the tide pole and on the north of Camel Rock.

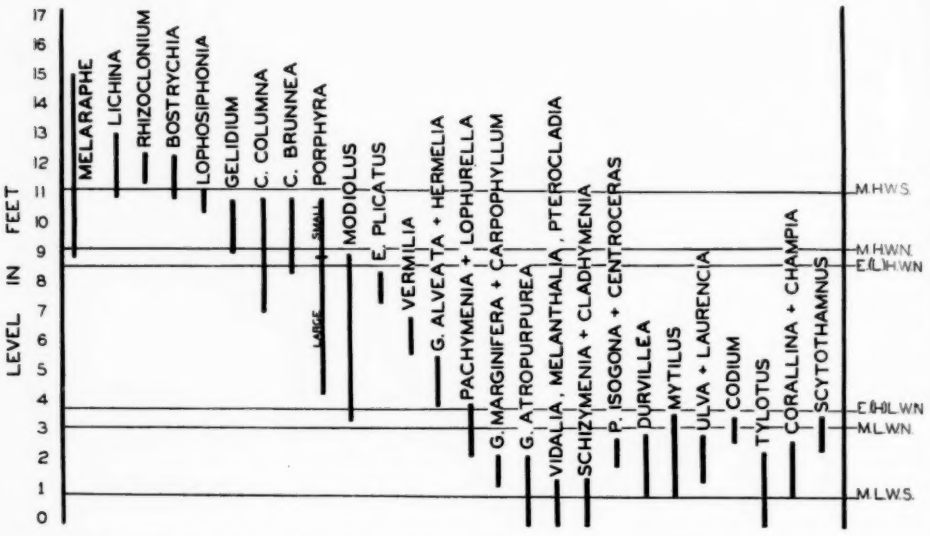

FIG. 13. Generalized vertical range of upper species at Piha after allowance has been made for the effect of wave action.

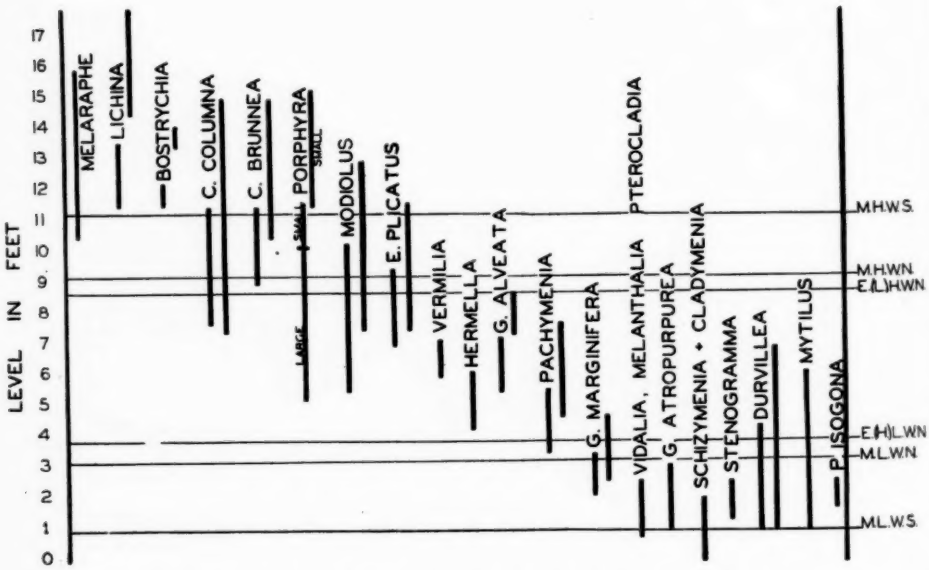

FIG. 14. Vertical distribution of dominant species at Piha generalized in positions of moderate shelter and exposure.

ures 5 and 6 will show that there is a change in total hours of exposure and also in total continuous exposure at this level.

The changes in total exposure and total continuous air exposure would seem to be the causal factors determining the six species with limits around + 9 feet. The species limits at E.(H).L.W.N. are very clearly defined and include those of three species important ecologically, e.g., *Pachymenia himantophora, Gigartina alveata,* and *Mytilus canaliculus.* Probably causal agents at this level are the changes in the total amount of air exposure and continuous submergence.

At M.L.W.N. *Durvillea* is the most important species ecologically and there are changes in the total amount of continuous submergence, the maximum period of continuous submergence, and the number of tidal submergences. At 2.3 feet the causal factors probably include total amount of continuous submergence and the total number of submergences. At M.L.W.S. the principal tidal factor appears to be changes in total air exposure, though at this level, and with the number of species involved, competition may be severe.

SUMMARY

A general account is given of the intertidal zonation at Piha on the west coast just north of Auckland. Eleven major biological communities are recognised, together with a few local or seasonal communities.

A levelling survey of the more important species was carried out, and after correlating the tides at Piha with those at Auckland, the principal tidal phenomena were worked out from actual tide charts. In most areas exposure to wave action elevated the limits of certain species, especially those higher up on the shore. If allowance is made for this elevation it is suggested that there are six critical levels at Piha; these are mean high water spring tides, about + 9 feet, extreme (highest) low water mark neap tides, mean low water neap tides, + 2.3 feet, and mean low water spring tides.

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Metamorphosis of the "Non-aquatic Frog" of the Palau Islands, Western Carolines

KENJI ATODA[1]

INTRODUCTION

THE FROGS in the Palau Islands seldom, if ever, leave their refuges during the daytime, but after sunset they are found easily in weedy places. There are two types of frogs, the large and the small, of which the larger is the female and the smaller the male. The male has strong jumping powers. Neither type has any webs between toes or fingers.

The adult frogs are well known to the Palau natives, who call them "gedegedug," "hedehedh," or "dechedech," but it is interesting to know that no one has seen their tadpoles. I made a search for the tadpoles in some pools and ponds, but without success, and the question soon arose as to where and how these frogs pass through their larval stages. During my long stay in the Palau Tropical Biological Station on Koror Island, I was fortunate several times in discovering the spawning place of the frogs, and was thus given the opportunity to study their metamorphosis.

Here I wish to express my thanks to Professor Shinkishi Hatai, then Director of the Palau Tropical Biological Station, for his kind guidance throughout the observations.

METAMORPHOSIS

The eggs collected from the natural spawning place were placed in a petri dish, the bottom of which was covered with a wet filter paper to maintain a humidity of about 100 per cent. The room temperature ranged from 25.1° to 31.0° C. throughout the period of observation.

The observations were made on one hatch, of which the youngest larva is shown in Figure 1*a*. The egg is covered with a rather tough gelatinous membrane and just after spawning it measures about 6 mm. in diameter. A large mass of yellowish-white yolk is attached to the abdomen of the larva. The three parts of the body—head, trunk, and tail—are distinguishable. The central part of the head is somewhat hollow, and rudimentary eyes appear on both sides. The mouth is a shallow invagination not yet open. The end of the tail is bent toward the abdomen. Each pair of limbs appears as rounded and protuberant swellings, the hind limbs being slightly larger than the forelimbs. Fine blood vessels run along the forelimbs, then toward the abdomen and finally branch into networks. The melanophores are not yet visible.

On the second day (Fig. 1*b*), a pair of well-developed eyes appears and the mouth opens, the tail becomes much longer, and the vascular system is conspicuously developed. The melanophores appear scattered over the head and trunk.

On the fourth day (Fig. 1*c*), the mouth is wide open and a pair of external nares is seen on its upper part. Numerous blood vessels are distributed over the abdominal region; the heart, which is perceptible through the skin, beats at an average rate of 120 times per minute (at a temperature of 30.8° C.).

On the seventh day (Fig. 1*d, e*), the yolk decreases and becomes flattened dorsoventrally. Five toes can be distinguished in the hind limbs but the forelimbs are hidden by the yolk mass. The melanophores increase in number on both the head and trunk.

On the tenth day (Figs. 1*f*; 2*a*), both the

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hind limbs and tail become more developed, and the latter reaches about 4 mm. in length. The body length, except for the tail, is about 5 mm.

On the fourteenth day (Fig. 2*b*), the egg reaches about 9.5 mm. in diameter. The egg seems to expand day by day as the larva grows in it. The skin of the abdomen, which begins to expand from about the seventh day of development, swells conspicuously and forms a pair of large, balloon-like sacs with a great number of blood vessels on the walls.

On the seventeenth day (Fig. 2*c, d, e*), the greater part of both tail and yolk are absorbed, and, except for the extreme expansion of the abdominal skin, the larva closely resembles an adult frog.

On the nineteenth day (Fig. 2*f*), nearly all of the yolk has been consumed and the tail is now rudimentary. When the egg is carefully removed from the vessel, the gelatinous membrane readily slips off and a miniature frog jumps free.

After a few more days all the larvae complete their metamorphosis, and as soon as they leave their eggs, the expanded abdominal skin contracts to adhere closely to the abdomen, showing the same appearance as in the adult frog. These young frogs measure about 6 mm. in length from the tip of snout to the anus.

ADULT FROG

Some of the external features of the male and female frogs are shown in Figure 3*a–e*.

Both types of frogs are dark brown but the male is the darker. The inside of the thighs is yellowish-red. In some frogs a fine line arises from the tip of the rostral and extends over the ridge of the back to the toe.

The tip of the rostral is somewhat rounded and the outer nostrils open close to its extremity. The distance between the rostrum and the point where the upper and lower jaws unite is slightly longer than the rostrum region. The distance between the extremity of the rostrum to the joint of each jaw is approximately equal to the width of head. The pupil is ellipsoid. The circular tympanum is conspicuous. Its diameter is about one and a half times the length between the hind margin of the eye and the fore margin of the tympanum, and is slightly shorter than the distance between each outer nostril. Close to the upper margin of the tympanum there is a narrow skin fold.

In the buccal cavity a pair of internal nostrils, a pair of triangular vomerine tooth plates, and a tongue are found. The tip of the tongue is bifurcated. The two types of frogs have tongues of different shapes; that of the large (female) frog is slenderer than that of the small (male) frog, and the distance between each small process is less in the large frog than in the small frog. There are minute teeth in the upper jaw but not in the lower jaw. The vocal sac is not very evident.

Some skin folds are scattered over the dorsal part of the trunk. Of the fingers of the forelimb, the third is longest, then the first is next longest; the other two fingers are nearly equal in length. Of the toes of the hind limb, the fourth is much more prominent than the others, and the first is shortest. The webs are completely degenerated. Many rounded protuberances of skin are found on the insides of the fingers, toes, palm, and metatarsus. The tips of both fingers and toes are rounded. The length from the base of the tibia to the tip of the longest toe is two and a half times that from the base of the arm to the tip of the longest finger, and is 1.6 times the length from the tip of the rostrum to the anus.

DISCUSSION

The eggs upon which the observations were made were collected in the months of May, October, and December. They were

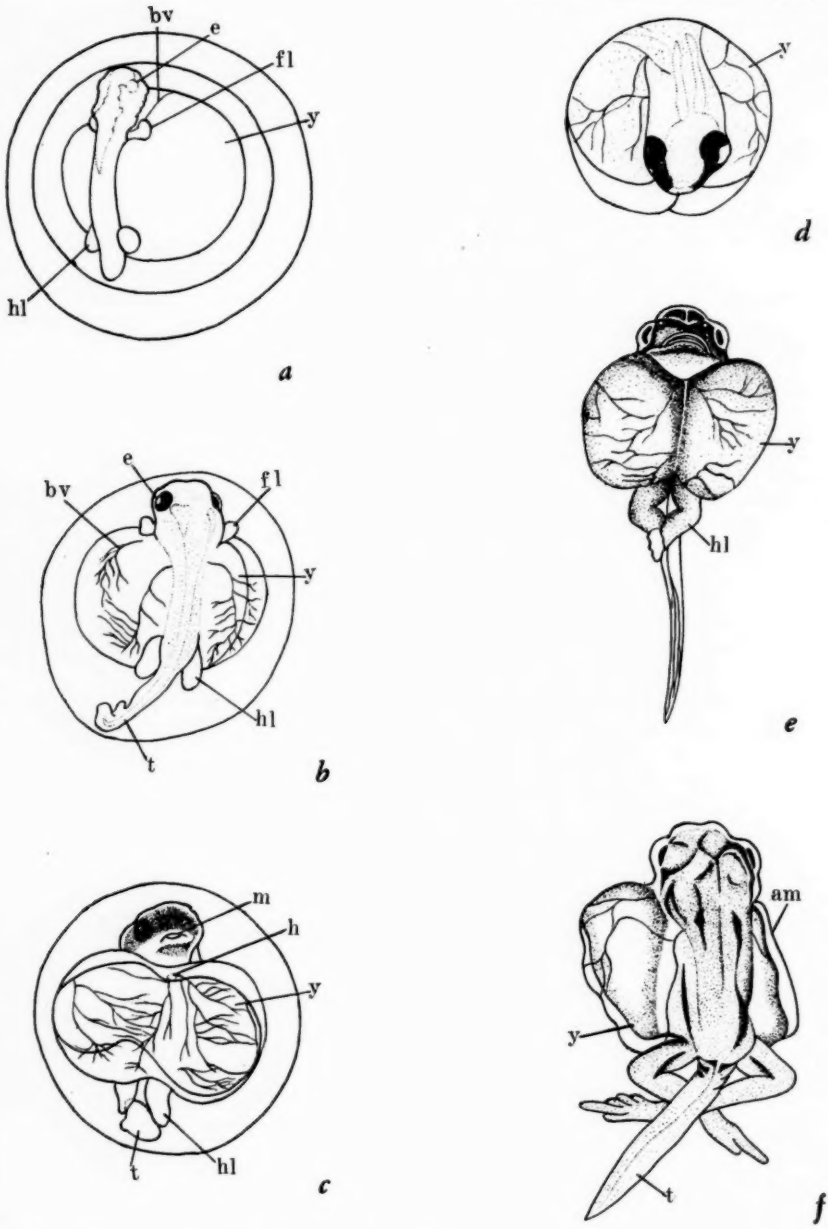

FIG. 1. Progressive stages of metamorphosis of the frog from the Palau Islands, × 7. *a*, Dorsal view of the youngest larva (the outer gelatinous egg membrane is omitted); *b*, 2 days later, dorsal view (only the innermost egg membrane is drawn); *c*, 4 days later, ventral view; *d*, 7 days later (all membranes are removed from the egg), frontal view; *e*, same as *d*, ventral view; *f*, 10 days later, dorsal view.

(am, Abdominal membrane; bv, blood vessel; e, eye; fl, forelimb; h, heart; hl, hind limb; m, mouth; t, tail.)

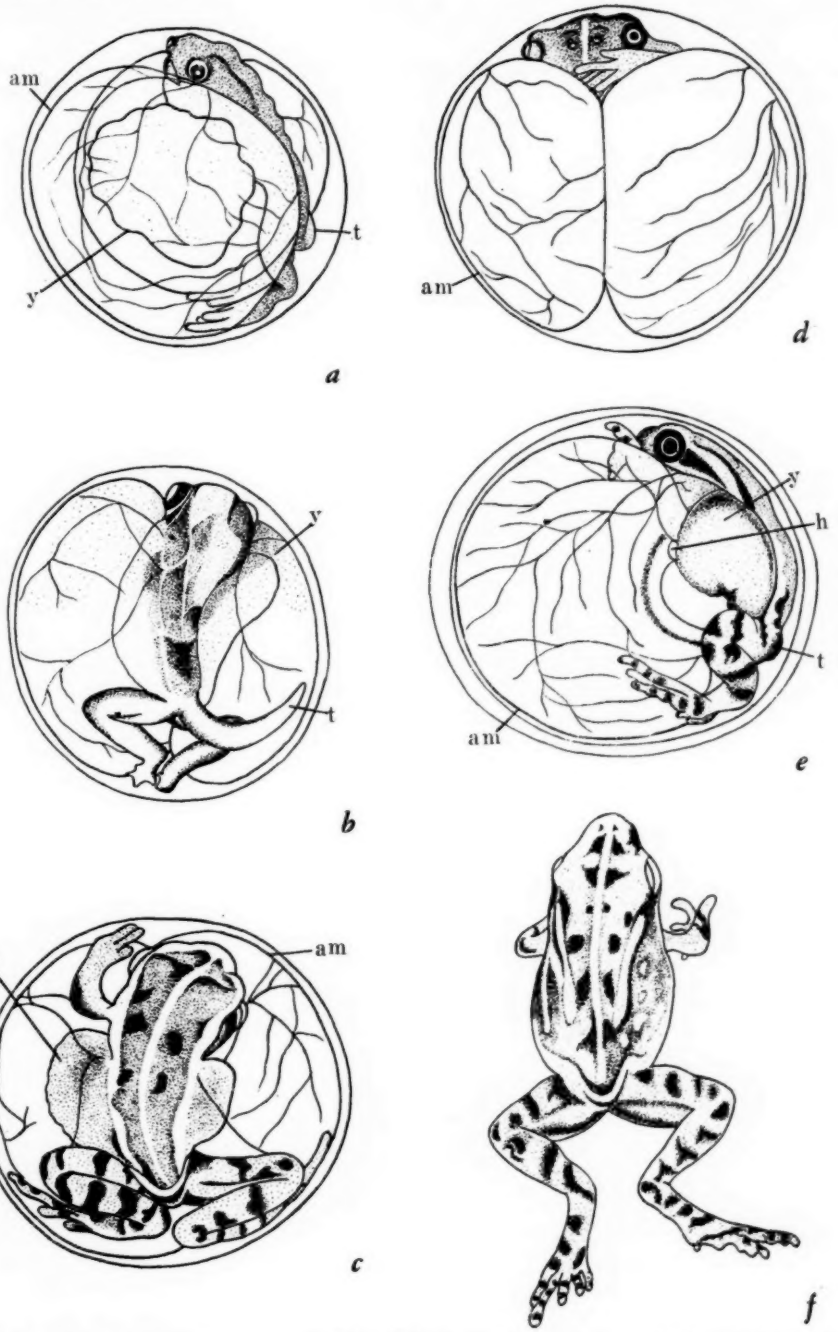

FIG. 2. Further stages in metamorphosis of the frog, × 7. *a*, Same as 1*f*, lateral view, only the innermost egg membrane is drawn; *b*, 14 days later, dorsal view; *c*, 17 days later, dorsal view; *d*, same as *c*, lateral view; *e*, same as *c*, ventral view; *f*, 19 days later, egg membranes removed, dorsal view.

spawned in a weedy place on the ground. The number of eggs in one hatch was usually about 30. At the time of each collection it was noticed that a considerable number of eggs with large yellow yolks could be seen through the skin in the abdomens of large frogs. These observations lead to the conclusion that the frogs have no definite spawning time, but spawn every month throughout the year.

Metamorphosis is completed so rapidly that the first stage observed was probably close to the earliest stage. Apparently, the time required to complete the metamorphosis is about 3 weeks.

The characteristic features of the metamorphosis of this frog are the extreme swelling of the abdominal skin and the absence of both external gills and gill clefts. The larva does not pass a free-swimming stage in water; therefore external gills for respiration are unnecessary. The larva grows rapidly within the egg, and metabolism takes place actively. The expansion of abdominal skin or the increase of body surface and the abundant blood vessels in the skin may be helpful in increasing respiration through the skin. In addition to these characteristics, the larva depends wholly upon the yolk for nutriment throughout metamorphosis, and its yolk is large, like that of a fish egg. Observations on the cleavage of the egg were not made.

Hitherto only two species of frogs have been known to exhibit behavior more or less similar to that of the Palau frog: *Hylodes* (= *Eleutherodactylus*) *martinicensis* (Peters 1876; Lynn 1940) and *Rana opisthodon* (Boulenger 1886). Both of them undergo their whole metamorphosis within their eggs, and their embryos possess neither gills nor gill openings.

Hylodes martinicensis lays its eggs on a broad leaf of a plant, and the eggs are then glued to the leaf. The egg measures 4–5 mm. in diameter. The metamorphosis is completed during 21 days, approximately the same time as was observed for the Palau frog. Its most noteworthy characteristic is the development of a large well-vascularized tail, the function of which is to serve as a respiratory organ, just as the extreme expansion of the abdominal skin of the Palau frog does for it.

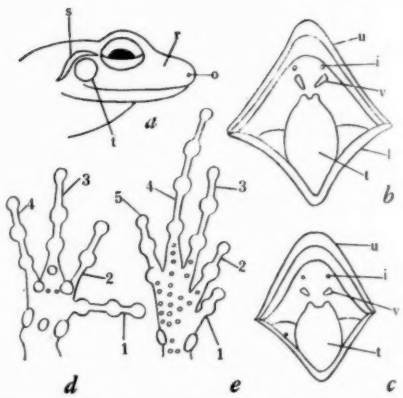

FIG. 3. Some external features of the adult frog. *a*, Lateral view of the head (approx. × 1.6; o, outer nostril; r, rostrum; s, skin fold; t, tympanum); *b*, buccal cavity of the large frog; *c*, same of the small frog (*b* and *c*, approx. × 2; i, internal nostril; l, lower jaw; t, tongue; v, vomerine tooth plate; u, upper jaw); *d*, palm and fingers (approx × 2.6; 1, 2, etc., the first, second, etc., fingers); *e*, metatarsus and toes (approx. × 2.6; 1, 2, etc., the first, second, etc., toes).

Rana opisthodon deposits its eggs in moist crevices of rock close to water. Its egg measures 6–10 mm. in diameter. Its embryo develops without any evidence of a tail, and has as breathing organs several regular transverse folds on each side of the abdomen which function in a manner quite similar to *Hylodes'* tail. Thus the Palau frog is entirely different from these two species.

At present it seems that the data are not sufficient to determine the genus to which the Palau frog belongs. Although both hand and foot well resemble those of *Hylodes,* the other general features rather resemble those of the Ranidae, and the frog probably is a new species of *Rana.* The two types of frogs

found, the small and the large, seem to indicate the occurrence of sexual dimorphism in the species.

SUMMARY

1. The frog described in this article is commonly found in the Palau Islands. There are two types, large and small, apparently an effect of sexual dimorphism. Neither type possesses webs between toes or fingers. This frog is probably a new species of *Rana*.

2. The number of eggs in one hatch is about 30 and they are spawned on the ground in weedy or bushy places. Metamorphosis is completed in the egg, and the frogs do not experience the free-swimming stage of a tadpole. About 3 weeks are required for complete metamorphosis.

3. During metamorphosis neither external gills nor gill clefts appear, but the abdominal skin expands to an extreme degree.

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On the Identity of *Spongocladia* and *Cladophoropsis*[1]

GEORGE F. PAPENFUSS[2]

IN THEIR TREATMENTS of the green algae in Engler and Prantl's "Die Natürlichen Pflanzenfamilien," Wille (1911: 119) and Printz (1927: 282) consider *Spongocladia* Areschoug (1853) as a genus of questionable merit. This belief was founded upon the observation of Weber-van Bosse (1890) that examples of *Struvea delicatula* which lived in association with the sponge *Halichondria* bore a great resemblance to *Spongocladia vaucheriaeformis,* the type species of the genus *Spongocladia.*

However, in a later work, Weber-van Bosse (1913: 86) not only maintained *Spongocladia* but emphasized that she had not demonstrated that *S. vaucheriaeformis* actually was a form of *Struvea delicatula* living in association with a sponge, and that there consequently was no justification for the statement of Wille *(loc. cit.):* "Nachdem es von A. Weber v. Bosse nachgewiesen worden ist, dass die typische Art: *S. vaucheriaeformis* Aresch. nur eine durch Symbiose mit einer Spongie *(Halichondria)* umgebildete *Struvea*-Art darstelle, muss auch die Stellung der 2 übrigen Arten: *Spongocladia dichotoma* (Zanard.) Murr. et Boodle, sowie *S. neocaledonica* Grun. als sehr zweifelhaft angesehen werden."

Even though there probably is no particularly close relationship between *Spongocladia* and *Struvea* Sonder (1845), both of which belong to the order Siphonocladales, but to the families Siphonocladaceae and Boodleaceae, respectively, I have on a number of occasions been struck by the agreement in the published descriptions and illustrations of *Spongocladia* and *Cladophoropsis* Børgesen (1905), both members of the family Siphonocladaceae. The purpose of the present article is to assemble the published facts and to record my own observations in support of the contention that these two genera of essentially tropical and subtropical marine algae actually are identical, a conclusion which Børgesen (1948) has also reached. Finally, *Cladophoropsis,* which is the better known genus, is proposed for conservation against *Spongocladia.*

The genus *Spongocladia* was erected by J. E. Areschoug in 1853 upon a new species, *S. vaucheriaeformis,* which he received from Mauritius. The plants grew upon encrusting corallines, forming a horizontal spongiose mass, from which issued erect, more or less dichotomously divided, spongiose growths. Both the horizontal and the erect portions of the thallus were composed of irregularly branched, septate, uniseriate filaments and, as shown in Areschoug's figure 3, the branches of the filaments lacked a cross wall at the base. Reproduction appeared to be by swarmers, many of which germinated within the cells in which they were produced. The thallus contained an abundance of sponge spicules, especially at the terminal ends of the erect portions.

Thirty years later the known geographic distribution of *Spongocladia vaucheriaeformis* was extended to Singapore by Hauck (1884). His study of the plant led him to the significant conclusion that systematically it belonged in the immediate vicinity of *Siphonocladus,* a genus which had been founded a few years previously by Schmitz (1879) to

[1]This study was made during the tenure of a Guggenheim Fellowship.

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accommodate two species, one of which was subsequently removed to *Cladophoropsis* by Børgesen (1905).

In 1888 Murray and Boodle published an account of the genus *Spongocladia* based upon a study of material of *S. vaucheriaeformis* from Mauritius and New Guinea and of two additional species from the south Pacific. They pointed out for the first time that the genus *Spongodendron* of Zanardini (1878), which was based upon two species (*S. crassum* Zanard. and *S. dichotomum* Zanard.) from New Guinea, was indistinguishable from *Spongocladia. Spongodendron crassum* was found to be identical with *Spongocladia vaucheriaeformis* whereas *Spongodendron dichotomum* could be maintained as a distinct species under the binomial *Spongocladia dichotoma* (Zanard.) Murray et Boodle. In addition, Murray and Boodle gave a brief account and the formal diagnosis of a new species from New Caledonia, *Spongocladia neocaledonica* Grunow, which differed from the others in having a compact thallus.

Up to the present no additional species of *Spongocladia* appear to have been described, but our knowledge of the genus has been enlarged in certain respects and the known geographical range of two of the species has been extended.

Heydrich (1894) reported *S. vaucheriaeformis* and *S. dichotoma* from the Ryukyu Islands, south of Japan. He was the first to bring attention to the fact that the thalli were not composed of a single plant but of a large number of individual *Cladophora*-like plants. In agreement with the observations of Zanardini and Murray and Boodle, he found that the filaments composing the thallus produced attachment organs, or tenaculae, by means of which they anastomosed with near-by filaments, forming a kind of network.

Heydrich was also the first to give an account of the method of formation of the so-called aplanospores (or coniocysts, as they had been called by Zanardini). He regarded *Spongocladia* as essentially a unicellular alga, which, like *Valonia,* formed aplanospores which produced daughter individuals that remained attached to the mother-plant. As we now know, the aplanospores of Heydrich were protoplasmic masses formed in consequence of segregative division, a characteristic feature of the order Siphonocladales. Like Hauck, Heydrich placed *Spongocladia* near *Siphonocladus.*

In 1913 Weber-van Bosse recorded *S. vaucheriaeformis* from Makassar and neighboring islands in the Dutch East Indies. She expressed the opinion that *Spongocladia* probably represented special forms of algae known otherwise by different names.

Okamura in 1916 recorded the occurrence of *S. vaucheriaeformis* at Ponape and Saipan in the Caroline and Marianas Islands, respectively. In a later work (1928), he confirmed the observation of Areschoug regarding the germination of spores (?) within the cells in which they were formed. He also saw and figured stages in their germination on the outside of filaments of the thallus. The germination of spores (?) within the reproductive structures was later observed by Yamada (1934) also. He appears to have been the first to have noted pores in the walls of the fertile cells, which suggests that the spores (?) are motile and that those which had been seen within the cells had merely failed to escape, as is so often true in the algae.

Although Okamura (1928) does not seem to have been fully aware of it, he clearly observed (see pl. 250, fig. 11) septation of the filaments by segregative division, thus confirming the observation (in the light of present knowledge) of Heydrich.

As far as I am aware, Dickie (1875), Jadin (1934), Lucas (1935), and Børgesen (1940, 1946, as well as 1948) are the only authors in addition to those already mentioned who have studied *Spongocladia.* Dickie, Jadin, and Børgesen included *S. vaucheriaeformis* in their lists of algae from Mauritius, whence

the species was first described, and Lucas reported it from Lord Howe Island.

In summary, then, a synthesis of the accumulated knowledge concerning the general morphology of *Spongocladia* reveals the following features as most characteristic of the genus:

1. The thallus is in the form of a prostrate, spongiose growth, which remains as a compact mass in *S. neocaledonica* or produces erect, branched, *Codium*-like processes in *S. vaucheriaeformis* and *S. dichotoma.*

2. The thallus is composed of intertwining, branched, septate filaments, with the cells arranged in a single series.

3. The branches of the filaments are not separated by a cross wall at the point of juncture with the parent filament.

4. Septation of the filaments is by segregative division.

5. The filaments form attachment organs, or tenaculae, by means of which they anastomose with other filaments, forming a kind of network.

6. Reproduction is by swarmers which are produced in the unmodified cells of the filaments.

These characters, with the possible exception of the first one listed above, indicate that *Spongocladia* Areschoug (1853) is identical with *Cladophoropsis,* a genus which was segregated from *Siphonocladus* Schmitz (1879) by Børgesen in 1905. This conclusion is supported by my own observations (particularly in regard to the absence of a cross wall at the point of attachment of the branches to the parent filaments) upon a species of *Spongocladia* (seemingly *S. vaucheriaeformis*) from the Philippine Islands and by those of Børgesen (1946, 1948) upon *S. vaucheriaeformis* from Mauritius. The agreement in the general appearance of the filaments composing the thallus in *Spongocladia* and *Cladophoropsis* is shown in Figure 1*a* and *b,* respectively, which are reproductions of illustrations by Børgesen from material gathered in the type regions of the type species of the two genera.

The observations of Børgesen in this connection are especially significant inasmuch as they were made, not only upon topotype material of the type species of *Spongocladia,* but by the author of *Cladophoropsis.* In 1946 (p. 17) he remarked: "According to my observations of the alga [*S. vaucheriaeformis*] it seems to me very like *Cladophoropsis,* for instance, *Cl. Zollingeri* . . ." and in 1948 (p. 24) he said, "the alga, being the biont of the sponge, is quite like that found in the formerly examined specimens, and thus in my opinion is a *Cladophoropsis.*"

Seemingly, the only difference between *Spongocladia* and *Cladophoropsis* lies in the general habit of the two genera. In *Cladophoropsis* the thalli are in the form of cushions, turfs, or tufts whereas in two of the species of *Spongocladia* (*S. vaucheriaeformis* and *S. dichotoma*) the basal prostrate system ordinarily produces erect, *Codium*-like portions. However, these differences are not constant and appear to be of a specific rather than a generic nature. Support for this contention is furnished by two facts: (1) In *S. neocaledonica* the thallus is in the form of a compact, barely branched growth, somewhat comparable to that of *Cladophoropsis membranacea* (Børgesen, 1913: 43 and 47) and certain other species in which the thallus is in the form of dense cushions or turfs. (2) Even in *S. vaucheriaeformis* the thallus may at times, according to Børgesen (1948: 23), be in the form of an extensive prostrate mat, with the erect portions reduced to conical growths of only 2–3 cm. in height.

Since the time that Børgesen (1905) erected *Cladophoropsis,* and transferred to it seven species which had previously been placed in *Siphonocladus,* the genus has been found to be well represented in tropical and subtropical waters, and to contain a few species which are known only from temperate regions. A search through the literature re-

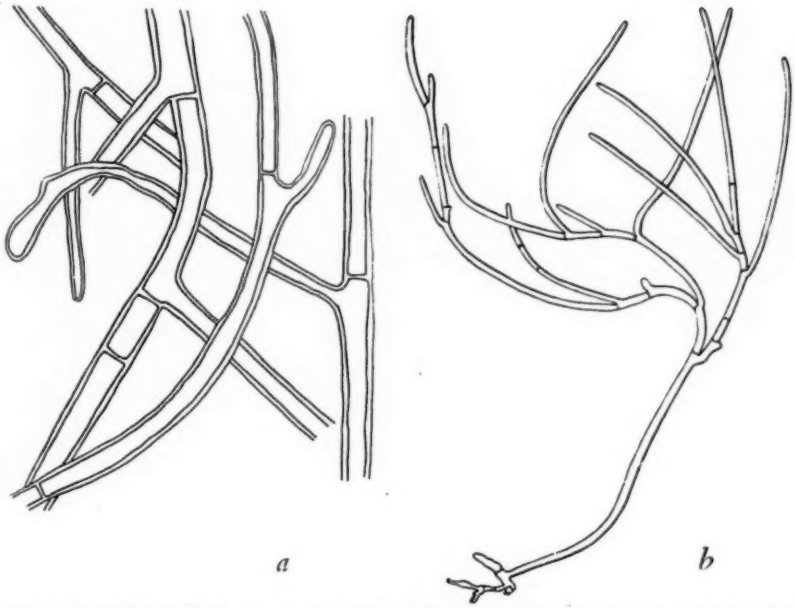

FIG. 1. *a, Spongocladia vaucheriaeformis:* filaments from the upper part of the thallus of a plant from Mauritius. × 45. *b, Cladophoropsis membranacea:* a part of the cushion-like thallus of a plant from the Virgin Islands. About × 5. (From Børgesen, 1948 and 1905, respectively.)

veals that up to the present some 19 species have been accredited to *Cladophoropsis.* They are: *C. brachyartra* (Sved.) Børgesen (1905); *C. fallax* Schiffner (1933); *C. fasciculata* (Kjellm.) Børgesen (1905); *C. gracillima* Dawson (1950); *C. herpestica* (Mont.) Howe (1914), incl. *C. coriacea* Yendo (*cf.* Yamada, 1944); *C. howensis* Lucas (1935); *C. infestans* Setchell (1924); *C. limicola* Setchell (1924); *C. macromeres* Taylor (1928); *C. membranacea* (Ag.) Børgesen (1905); *C. modonensis* (Kütz.) Børgesen (1905); *C. pallida* Baardseth (1941); *C. peruviana* Howe (1914); *C. psyttaliensis* (Schm.) Børgesen (1905); *C. rigida* (Howe) Feldmann (1938); *C. robusta* Setchell et Gardner (1924); *C. sundanensis* Reinbold (1905); *C. voluticola* (Hariot) Børgesen (1905); and *C. Zollingeri* (Kütz.) Børgesen (1905).

Considering the wide recognition which *Cladophoropsis* has received in the course of the past 45 years as contrasted with *Spongocladia,* which has been referred to in a comparatively small number of publications, it would be advantageous to reject the latter name in favor of the former, and it is accordingly proposed that *Cladophoropsis* be considered for conservation.

CLADOPHOROPSIS Børgesen (Siphonocladaceae), K. Danske Vidensk. Selsk. Forhandl. 1905: 288, 1905.

versus

Spongocladia J. E. Areschoug, Öfvers. K. Vetensk.-Akad. Förhandl. 10: 202, 1853.

Type species: *Cladophoropsis membranacea* (Ag.) Børgesen.

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Luminous Organs of Fish Which Emit Light Indirectly

YATA HANEDA[1]

INTRODUCTION

THERE ARE MANY REPORTS of luminous fishes, all of which, in earlier days, were taken from the deep seas. Luminous organs were found on the sides of the bodies, on the barbels, or on the antennae. In outward appearance these fishes were strangely shaped and feebly developed, with soft bones and loose muscles, and it was assumed that such unusual fishes belonged exclusively to the deep-sea fauna.

The material examined was invariably dead and damaged. It might have been newly caught, or else had been preserved in formalin or in alcohol for an indefinite period.

There seems to be very little record of observations on living material, and only the morphology of the organs of these fishes was studied. The organs were never really understood, and were mistaken for sensory organs, electric organs, or secondary eyes, or they were simply referred to as eye-like organs.

In the early days bacteriological knowledge, especially knowledge of luminous bacteria, was not far advanced, and fish which became luminous after death as a result of contamination by saprophytic luminous bacteria were mistaken for true luminous fishes.

Recent advances in the study of these interesting problems of luminosity have shown that luminous fishes are not confined to the deep-sea fauna, but may be found among the fauna of the shallow and coastal waters of the sea, and that luminosity may be caused by luminous bacteria. Moreover these studies have revealed that luminous bacteria play an important role in the production of light in some fishes by entering certain ducts possessed by these fishes, and there settling down to a symbiotic existence. Within the duct they are cultured and utilized as a source of light, the fish undergoing some modifications to create an organization within itself to display the light. Such an association between a fish and luminous bacteria constitutes what is known as luminous symbiosis.

Most known luminous fishes are found in deep oceanic waters and have on the surface of their heads or bodies, or on their barbels, or on their antennae, curious arrangements of luminous organs of varied shapes, sizes, and arrangements. For example the luminous sharks have on the side of their bodies simple, small luminous dots which consist of groups of luminous skin organs. The genera *Stomias, Chauliodus,* and *Gonostomias* also possess numerous luminous dots in the underlying skin in addition to their regular series of luminous organs. A *Porichtys* species has rows of many small luminous organs which follow the direction of the multiple lateral lines. A *Pseudoscopelus* species has numerous minute luminous organs arranged in indefinite rows of a characteristic shape. The lantern fishes (Myctophidae) possess fewer luminous organs, but these are pearl-like and are arranged symmetrically in a series on each side of the fishes. In some species of *Lampanyctus,* luminous scales may be present above or below the tail base. Luminous patches or ducts occur on the head of *Diaphus* or on the body of *Lampanyctus* species. The Sternoptychidae and Stomiatidae are characterized by highly developed luminous organs of a more complex structure, consisting of a luminous body, reflector, lens, and color fil-

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Manuscript received January 26, 1949.

ter. In addition to the serial luminous organs on the body there may be luminous organs on the jaws and near the eye. The more complex postocular organ of the Stomiatidae is freely movable, and can be rolled inward when not required.

In the families Stomiatidae and Malacosteidae there is a barbel which, in *Diplolychnus,* is luminous at the end. In many other species, however, it is not certain whether this barbel is luminous or not.

Deep-sea angler fishes have a luminous antenna. *Lamprotoxus* has a closed loop of luminous tissue on each side of the body between the head and pelvic region, while in *Eurypharynx* and *Saccopharynx* there is a looped luminous organ which extends along each side of the dorsal fin as far as its posterior extremity, beginning either just behind the skull or just in front of the anterior extremity of the fin. There is a half-moon-shaped luminous organ which is freely movable and which can be rolled inside situated below the eye in *Anomalops. Photoblepharon* can shut off the luminous part of the organ by lowering a black membrane which functions like an eyelid. A species of *Dolichopteryx* has a luminous organ on the ball of the eye in front of the lens. *Monocentris japonicus* has a pair of luminous organs on the end of the jaws. Some species of the families Gadidae and Macrouridae possess a luminous organ ventrally in front of the anus.

All of these mentioned luminous organs are of the direct emission type. That is, their luminescence is emitted directly from the source (the luminous body) and remains more or less concentrated or focused at one point without much diffusion.

Some luminous fishes show no outward peculiarities in structure or appearance and resemble ordinary non-luminous fish. This is because the luminous body lies inside the fish and cannot be seen. Before its light can be seen it must first be directed to a reflecting surface within the body. The light is reflected to pass through a considerable lateroventral translucent area of lenticular muscles where it appears as a diffused bluish glow. This diffusion may be compared with the effect which a frosted or "opal" bulb of an electric lamp has in screening the glare of the incandescent filament and reducing it to a diffused glow. As far as is known this indirect emission type is confined to *Acropoma* and the Leiognathidae.

These fishes differ from other luminous fish in possessing unusually large luminous areas. In fact they utilize half the muscles of their complicated body structure for this purpose. Recently Kato (1947) discovered that *Apogon marginatus* Döderlein, belonging to the family Apogonidae, also possesses this same type of luminous organ.

I have made a study of luminous fishes since 1933, and have collected considerable material in Japan and in more southerly regions. Subsequent to 1937 I worked at the Palao Tropical Biological Station on several occasions during which I took the opportunity to visit the Philippine Islands, North Borneo, New Guinea, Celebes, Java, Sumatra, and Malay, where I collected many specimens of living luminous tropical fishes and observed their luminosity.

Acknowledgment: I wish to express my hearty thanks to Dr. S. Hatai, former Director of the Palao Tropical Biological Station and to Dr. Y. Tokugawa, Tokugawa Biological Institute. My thanks are also due to Mr. W. Birtwistle, former Director of the Fisheries Department of Singapore and Federated Malay States, who helped me in many ways during my stay in Singapore. I must express my sincere gratitude to Dr. D. J. Pletsch, Scientific & Technical Division, ESS, GHQ, SCAP, who assisted me in obtaining publication of this paper.

LUMINESCENCE IN *Acropoma japonicum*

Material

Acropoma is a genus of fishes of the family

Acropomidae found in the Sea of Japan and the Philippine Sea. Two species are known: *Acropoma japonicum* Günther, and *Acropoma philippinense* Günther. *Acropoma philippinense* was found near the Philippine Islands by the "Challenger" at a depth of 82 to 102 fathoms. *Acropoma japonicum* is known as "Hotaru-jako" in Japan, and is considered there to be a single species.

I have examined a large number of these "Hotaru-jako" in a fresh condition and believe that there are two species (Haneda, 1939) but in the absence of confirmation of this belief by an ichthyologist, I refer to them as Type I and Type II (Figs. 1 and 2). They both occur in the southern Japan Sea as a mid-water dweller in a depth ranging from about 80 fms. to 200 fms. They are beautifully rose colored and attain a length 200 mm.

If these two types are examined in detail many differences are found, not only between their external characters, but also between their luminous organs. For example:

Type I is colored pale red dorsally, and whitish ventrally.

Type II is a beautiful purple-red dorsally, and ventrally is light purplish-red.

Both possess many chromatophores on the ventral sides but Type II possesses the greater number.

The scales of Type I are firmly fixed in the body, while in Type II they are extremely deciduous; for this reason it is very difficult to obtain in the public fish markets specimens of Type II with scales attached.

The anus in Type I is situated approximately under the third spiny ray of the dorsal fin, but in Type II it is situated below the hindmost edge of the end of the dorsal fin.

The anus in Type I is white and in Type II it is strongly black pigmented.

Type I is furnished with a pair of canine teeth which Type II lacks.

Type I occurs in water of about 80 fms. in depth, while Type II occurs in waters more than 100 fms. deep. They are very seldom taken together by trawling vessels.

The greatest difference, however, lies in the size of the U-shaped internal luminous gland. That of Type I is short, with the ends directed posteriorly; while that of Type II is much longer, with the free ends directed anteriorly.

These differences, I suggest, justify the creation of a second species, but I prefer to call the two kinds of fish Type I and Type II. I have examined many specimens of both types, as well as males and females of each type. The gonads of Type I are full in October and those of Type II from December to February. All ichthyologists have considered them to be the same species, *A. japonicum*, and Type II only a variety of Type I, but in my opinion each is a distinct species.

During the winter season they are caught by trawlers in the Gulf of Tosa off Shikoku Island, Japan, in depths varying from 80 to 200 fathoms, and there is no difficulty in obtaining specimens in the Mimase fish market near the city of Kōchi, Shikoku Island. During each of the winters of 1934 to 1940 I obtained many specimens in this fish market. In Mimase and Urado near Kōchi, they are called Hotaru-jako, meaning "the small firefly fish," or Kigane-jako, and the fishermen who catch them during the night are aware of the luminosity in their ventral regions, as are most of the ichthyologists, who state that the luminosity is due to the numerous small black points on the ventral surface of the body. These they consider are skin organs similar to those of the luminous sharks, but they do not describe their structure.

It was not until I had dissected many fresh specimens that I discovered the peculiar luminous organs established in them and perceived that the small black points which had

been believed to be small luminous organs were nothing more than chromatophores.

The luminous organs consist of the following five components: a U-shaped luminous filiform body; an external opening of the canal of the luminous body; a reflector; a series of lenses; and a means of controlling the display of luminescence.

Luminous Organ of A. japonicum *Type I* (Fig. 1)

Luminous Gland—The luminous gland is a whitish-yellow U-shaped filiform body, like a U-tube, lying flat and embedded in the muscles of the pectoral and ventral regions. Each "limb" of the tube is sealed at its end. The bend of the tube lies nearer the head than the closed ends of the "limbs" or filaments. This bent filament has an outer layer of longitudinally arranged fibers, an inner layer of circularly arranged fibers, and an innermost folded glandular epithelium, which surrounds a hollow duct or cavity. It is pierced on the

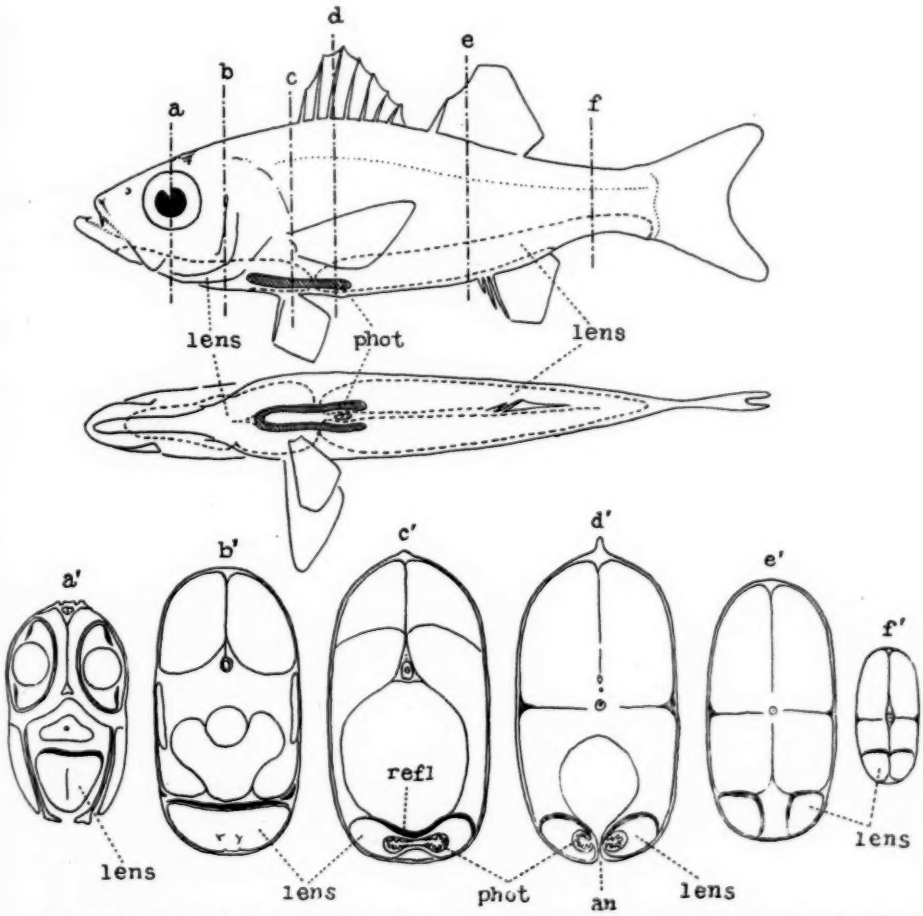

FIG. 1. Diagrammatic figure of the luminous organ of *Acropoma japonicum* Type I: phot, luminous gland; lens, lens; refl, reflector; a', b', c', d', e', f'—transverse sections at a, b, c, d, e, and f.

inner faces of the limbs by numerous capillary ducts which enter a larger central canal lying between the inner faces of the limbs of the U-tube. This canal is bounded dorsally and ventrally by concave membranes and has only one opening, which is at the anus. The whole luminous gland from a specimen 145 mm. long measured 14 mm., and from a fish 110 mm. measured 13 mm.

External Opening—In the gland, bacteria occur in the film of material which lies on the inner surface of the epithelial cells. These bacteria are present in clusters or else are attached to the surface of the gland cells. They pass from there into the duct or cavity of the U-shaped gland via the gland ducts. Here they remain until they pass through one of the numerous capillaries or pores into the larger central canal which opens in front of the anus. This is the only external opening of this canal. A luminous organ with an opening of this type is known as an open type of luminous organ.

Reflector—The reflector is a white, opalescent, opaque membrane lying above the luminous duct and extending from the isthmus to the end of the caudal peduncle. It lies rather low ventrally, and separates the lower ventral or keel muscles from the upper lateral and dorsal muscles. It passes below the pericardial and perivisceral cavities; under the latter it is depressed and forced downward into a concavity. Elsewhere it lies flat.

Lens Structure—The lower ventral or keel muscles below this membrane are lenticular and modified to transmit light. They are translucent but cloudy. They lie longitudinally and in pairs, i.e., one pair on each side. The first pair extends, one on each side, from the isthmus to the anus. The second pair lies, one on each side, from the anus to the end of the caudal peduncle. As they lie extended they may touch each other in places, but where they are not in contact they are separated by non-translucent muscle of ordinary structure. The luminous gland passes through these muscles, and each limb passes backward, one on each side, the bend being in the anterior part of the body of the fish, and the closed ends of the limbs being directed backward in the direction of the anus. When I made complete cross sections of fresh fish, I noticed that where I had cut through the limbs of the organ, the luminosity was brilliant; it was only moderate and diffused in the muscles which were cut. The light was screened by the reflecting membrane above, but was reflected downward and laterally through the skin of the fish. Where I cut a cross section of a fish without cutting the limbs of the luminous gland, the muscles surrounding the limbs appeared to be luminous, suggesting that the muscles themselves were luminescent.

Light Control Mechanism—This luminous organ has in itself no regulating mechanism for controlling the display of light. On the other hand, the ventral area and lower lateral area below the reflecting membrane are furnished with a great number of chromatophores in the surface of the skin. Above the membrane this particular kind of chromatophore disappears and is replaced by another kind. The former are the chromatophores which at one time were considered to be the actual luminous organs, but by their contraction and expansion they probably control the amount of light emitted.

Luminous Organs of A. japonicum *Type II* (Fig. 2)

The luminous gland is situated in the ventral muscle and is long compared with that of Type I. It extends from the isthmus to about the 5th ray of the anal fin, where it bends with a short loop on each side of the fin. These loops are directed obliquely downward, and continue in a reverse direction for a short distance where the bend is continued to the center. In this way the two limbs form a kind of hooked loop, such as would be

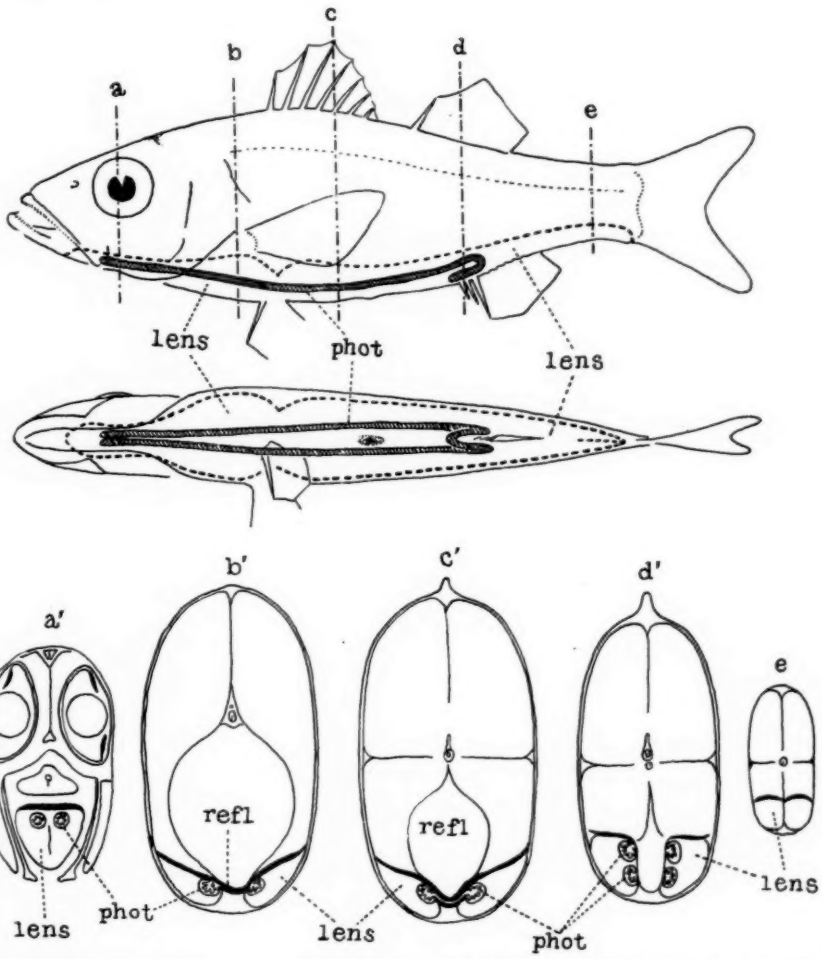

FIG. 2. Diagrammatic figure of the luminous organ of *Acropoma japonicum* Type II: phot, luminous gland; lens, lens; refl, reflector; a', b', c', d', e'—transverse sections at a, b, c, d, and e.

made if the closed end of a hairpin were bent over to form a hook.

The free ends of each limb of this organ lie in the isthmus, and the arrangement is a complete reversal of that found in Type I. The gland is reddish-yellow when fresh. Structurally it is similar to that described for the fish of Type I.

The central canal between the inner loops continues beyond the anus and opens into the cloaca through an opening which completely encircles it.

The muscles which form the lenses are comparatively poor as lenses when compared with those of the Type I fish, but are similar in other respects and equally translucent. The chromatophores are extremely numerous in the ventral region, and there are many more of them than in the fish of Type I.

These two types of luminous organs of

Acropoma japonicum are peculiar organs of a new type. The luminous glands are situated in the muscles, and they may be considered as an indirect or reflecting type of luminous organ functioning by reflected light.

Remarks on the Luminescence

Since the luminous gland is not visible on the surface of the body, both types of fish, externally and in daylight, have the appearance of ordinary non-luminous fish.

In the dark, however, e.g., when caught alive in a net at night, the ventral area is brilliantly illuminated. The luminosity is continuous, never disappearing completely, but may be dimmed by means of the chromatophores.

When the fish are recently dead the luminosity persists in both types, but gradually becomes dim. One or two days after death the muscles become opaque and are no longer translucent, and then the luminosity is extremely dim. If, however, after this period, the luminous glands are removed it will be seen that their luminosity persists as brilliantly as before and can even be seen in daylight by shading the glands in the cupped hands.

Remarks on the Substance in the Luminous Glands

To examine the substance in the glands, I made emulsions of it in distilled water, in 0.5, 2, 3, and 4 per cent NaCl solutions, and in sea water. These emulsions were kept at 18°–23° C. and were examined in the dark.

The sea water emulsion was the most luminous; next in order were the 3 per cent NaCl, the 4 per cent NaCl, the 2 per cent NaCl (which was rather weak), and the 0.5 per cent NaCl (which was extremely weak). The distilled water emulsion was not luminous.

The temperature of the sea water emulsion was lowered to 0° C., at which temperature it showed only a weak luminescence, but recovered its strength when warmed to 18° to 23° C., within which range it was strongest. At temperatures above 30° C. the luminosity diminished until at 45° C. it was no longer visible. When cooled it regained its luminescence, but it was lost again below 0° C.; however, luminescence was again recovered when the emulsion was warmed.

The Luminous Bacteria

When the emulsion of the gland was ex-

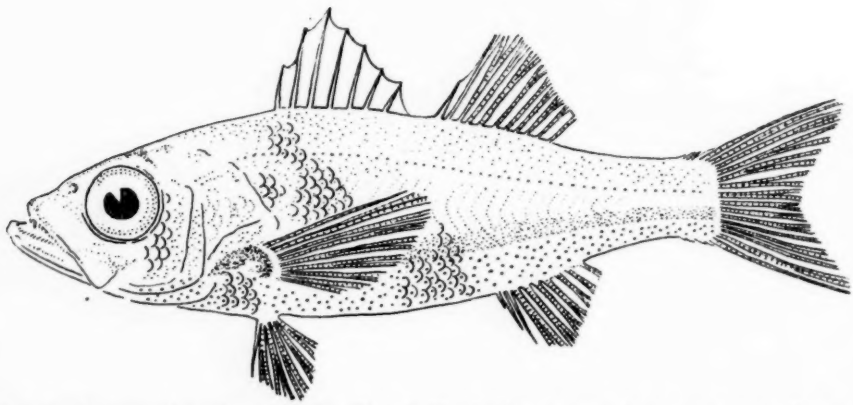

FIG. 3. *Acropoma japonicum* Günther Type I. The luminous organ is not seen externally, so that the fish looks like a common non-luminous one, but the lower part of the fish body is a lightning-like bluish-white color.

amined microscopically a large number of bacteria and some duct cell fragments could be seen. In the latter could be seen what were apparently bacteria since they stained well with Ziehl's solution and were Gram negative. Bacteria which had been taken from the luminous gland and cultured in media were tested for luminescence in the same solution as were the emulsions.

One hundred different strains of the luminous bacteria were obtained by the usual bacteriological techniques from 100 of each of the two different types of *Acropoma japonicum*. The cultures of bacteria taken from each of the types of fish showed some differences. On the basis of preliminary tests it appears that they represent two heretofore unknown species of bacteria which will be discussed at length in a separate paper. I tested the agglutination reactions of representative strains of these two new kinds of bacteria, and they showed a strain specificity similar to that of other symbiotic luminous bacteria (Kishitani 1930, 1932; Yasaki and Haneda, 1936).

LUMINESCENCE IN THE FAMILY LEIOGNATHIDAE

Material

The fishes belonging to the family Leiognathidae are true shallow-water forms, and are abundant in the southern Sea of Japan and in tropical seas. When I published my account of the luminescence of these fishes in 1940 I was not aware that their luminescence was already known, and it was only by chance that I found, in 1943, a reference to the work of J. W. Harmes in *Biological Abstracts* in the Raffles Museum Library. It is an abstract of a paper which appeared in 1928, entitled "Bau und Entwicklung eines eigenartigen Leuchtorganen bei *Equula* spec." Unfortunately I have not yet been able to see the full account of this discovery. However, while working independently on luminous organisms of the South Sea Islands at the Palao Tropical Biological Station, I discovered that *Gazza minuta* and several other species in this family are also luminescent when alive. The Leiognathidae living in shallow waters are not provided with externally visible luminous organs and superficially they resemble ordinary non-luminous fishes. For this reason their luminosity was unexpected.

Besides *Gazza minuta* I collected 15 other species of the Leiognathidae. Investigation of these species reveals that they all possess a luminous organ of a type similar to that of *Gazza minuta*.

Since the luminescence of these fishes of the family Leiognathidae was, I thought, unknown, I published the results of my investigations in 1940. I now present the results in revised form.

Gazza minuta occurs in clear water in Palao at a depth of about 30 meters and *Leiognathus equulus* lives in turbid water in the vicinity of mangrove trees at a depth of 1–2 meters. In Palao and Yap, *L. equulus* ranged in length from 60 to 70 mm.; in Ponape it was 180 mm. long; and in Sandakan, 200 mm. long. In Sandakan, the Chinese fishermen catch these fishes in nets and bring them every morning for sale in the Sandakan fish market.

In Japan there are three species, *L. argenteum* (Japanese name Uchi-Hiiragi), *L. rivulatum* (Oki-Hiiragi), and *L. elongatus* (Hime-Hiiragi).

L. argenteum and *L. rivulatum* are common on the southern coast of Japan. They are extremely abundant in Nagasaki where they are called Gira-gira or Gira. In Kōchi they are called Nirogi. In the bay of Urado near the city of Kōchi many old men may be seen fishing for Nirogi on any fine autumn day. *L. argenteum* is caught almost entirely by hook and line. This species lives in rather turbid water along the shores of the river estuaries, and it is from this fact that the

TABLE 1
DATA ON COLLECTIONS OF LUMINOUS LEIOGNATHIDAE

SPECIES	PLACE OF COLLECTION	DATE OF COLLECTION
Gazza minuta (Bloch)	Palao	June 1937, Feb. 1938
Koban-Hiiragi (Japanese)	Yap	August 1937
Kekek, Kekek labu (Malay)	Sandakan, B. N. Borneo	March 1938
	Ponape	March 1940
	Singapore	March 1943, Nov. 1944
	Penang, Malay	June 1943
	Batavia	March 1945
Secutor insidiator (Bloch)	Sandakan, B. N. Borneo	March 1938
Secutor ruconius (Ham.-Buch.)	Sandakan	March 1938
Ukekuchi-Hiiragi (Japanese)	Singapore, Penang	June 1943
	Batavia	March 1945
Leiognathus equulus (Forsk)	Palao, Yap	June, Aug. 1937; Feb. 1938
Seitaka-Hiiragi (Japanese)	Truk	March 1940
Kekek gadabang (Malay)	Ponape	March 1940
	Sandakan	March 1938
	Itoman, Okinawa	March 1938
	Singapore, Penang	June 1943, Aug. 1944
	Batavia	March 1945
L. fasciatus (Lacép.)	Palao	June 1937, Feb. 1938
	Ponape	March 1940
	Truk	March 1940
	Sandakan	March 1938
	Singapore	Sept. 1943
L. lineolatus (Cuvier & Valenciennes)	Palao	Oct. 1937
Ito-Hiiragi (Japanese)	Palao	March 1940
	Palao	Oct. 1943
L. splendens (Cuvier)	Sandakan	March 1938
	Singapore	Sept. 1943
L. daura (Cuvier & Valenciennes)	Sandakan	March 1938
	Singapore	Oct. 1944
L. bindus (Cuvier & Valenciennes)	Davao, Philippines	Aug. 1939
L. berbis (Valenciennes)	Singapore	Nov. 1943
L. dussumieri (Cuvier & Valenciennes)	Singapore	Oct. 1944
L. stercorarius Evermann & Seale	Singapore	Nov. 1944
L. elongatus Günther	Izu, Japan	Oct. 1938
Hime-Hiiragi (Japanese)		
L. rivulatum (Temminck & Schlegel)	Tosa, Japan	Oct. 1939
Uchi-Hiiragi (Japanese)		
L. argenteum (Lacépede)	Tosa, Japan	Oct. 1939
Oki-Hiiragi (Japanese)		

species derives its name of Uchi Nirogi—inshore nirogi. It is always present in the street markets. *L. rivulatum* occurs in the off-shore waters, and is taken only in nets. It is plentiful in the Mimase fish market near the city of Kōchi. Both species are usually dried for sale, and are very good to eat.

L. elongatus is not common. It is also an off-shore species. I obtained my specimens off Suzukawa–Shizuoka Prefecture.

From the Itoman market, Ryukyu Islands, I obtained two specimens of *L. equulus* and

Gazza minuta. Both specimens were the same as those found in tropical seas.

In 1943–1944 I collected in Singapore the species as listed in the accompanying table.

Around Singapore and the Malay Peninsula these kinds of fishes are easily obtained in all seasons from the fishing trap known as the Kelong. Fowler (1938) reported 12 species of this family in Malaya.

The Luminous Organ

Gazza minuta: Externally this fish does not present any unusual features, and it was only by a careful observation of the living fish by night that the bluish-white luminescence of the lower half of the body was revealed.

The source of the luminescence is a swollen ring of gland-like substance which encircles the oesophagus. It is covered with a white membrane except at two points, one located dorsally and the other ventrally. These appear as two small bean-shaped areas of a yellowish-white color. The ring contains a gland which has two openings (Fig. 4, op) which lead into the oesophagus.

The swim bladder and the thoracic and ventral muscles are so modified as to increase the efficiency of the light-producing mechanism. The swim bladder is lined with a remarkably bright silvery reflecting surface and the muscles of the thorax and the ventral parts of the body are translucent but somewhat cloudy. The swim bladder has no reflecting surface at its posterior end, which is translucent. Part of the dorsal silver lining is continued under the spinal column and acts as a reflector for the light which is transmitted backward through the translucent end of the bladder. Light is emitted from the two bean-shaped areas only, the dorsal one illuminating the swim bladder, the ventral one the thoracic and ventral muscles.

If the diagram of the longitudinal section of the fish through the swim bladder is studied, it will be seen that the anterior end of the swim bladder forms a parabola, and that a bean-shaped light spot (one part of the luminous ring gland) is at its focus. We

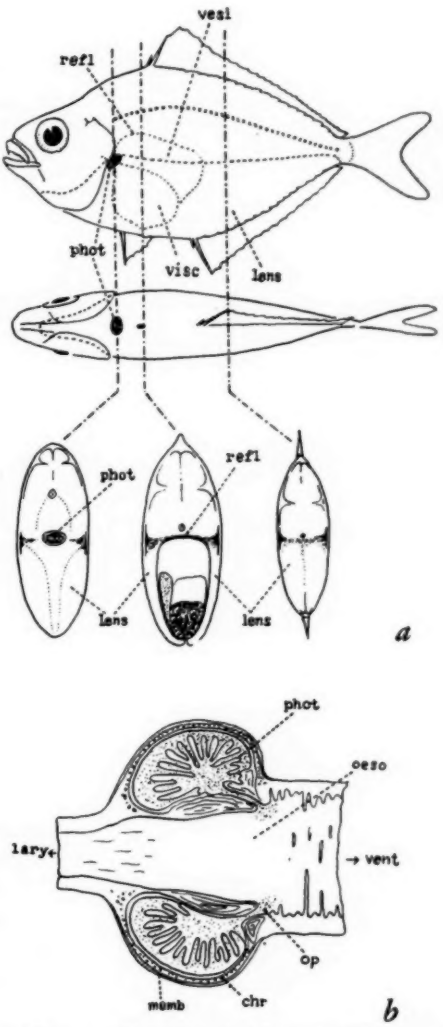

FIG. 4. *a*, Diagrammatic figure of the luminous organ of *Gazza minuta* (Bloch). *b*, Longitudinal section of the luminous gland of *Gazza minuta* (Bloch): phot, luminous gland; refl, reflector; lens, lens; visc, internal organ; vesi, swim bladder; chr, chromatophore; memb, membrane; op, opening of luminous gland; oeso, oesophagus; lary, larynx; vent, stomach.

have, in fact, a remarkably efficient parabolic reflector which reflects the emitted light backward even as far as the muscles of the caudal peduncle.

The ventral light spot directs its light downward, and, because of the cloudy translucent muscles of the thorax and abdomen, a diffused luminescence is seen in this area. Because of the presence of a white opaque membrane extending dorsally from the upper borders of the abdominal muscles of both sides, no light reaches the dorsal part of the body.

The bean-shaped areas are furnished with chromatophores, and it is perhaps due to their expansion that the light can be shut off, and by their contraction displayed. Possibly the white membrane which covers the ring can be contracted to cover the light spots, but this I was unable to confirm. Normally it is expanded to uncover them.

The complete luminous organ therefore consists of three components, possibly four: (1) the luminous ring gland; (2) the reflector; and (3) the lenses; with possibly (4), a shutter for the light spots which may be opened or closed either by the chromatophores or by the white covering membrane of the ring working independently or simultaneously with the chromatophores. In recently dead specimens these spots are closed by the membrane, but the gland material is still luminous.

As previously stated this fish differs from other luminous fish by its unusually large luminous area, utilizing in fact half the muscles of its extremely complicated body structure. The luminous glands are situated in the body, and may be considered to be of an indirect or reflecting type, functioning by reflected light in the same way as described for *Acropoma japonicum*; but *Gazza minuta* is not only provided with a membrane and chromatophores for displaying its luminescence, it has a far more complex luminous organ than *Acropoma japonicum*.

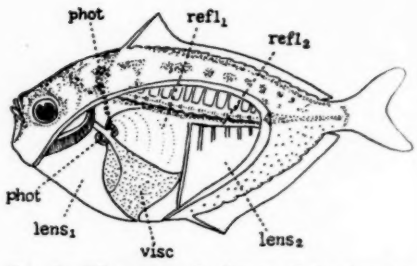

FIG. 5. Diagrammatic figure of the luminous organ of *Secutor insidiator:* phot, luminous gland; refl$_1$, refl$_2$, reflectors; lens$_1$, lens$_2$, lenses; visc, internal organs.

Secutor spp.: *Secutor insidiator* (Fig. 5) and *S. ruconius* are luminous Leiognathidae, similar to *Gazza minuta,* but possessing a relatively larger luminous gland than does *G. minuta.* It is yellow in fresh material instead of white as in *G. minuta.*

The reflector is very efficiently arranged and is lined with a bright glossy surface.

The ventral muscles are cloudy and translucent. The ventral cavity walls are extremely thin and, because of this, its luminosity is greater than that of any of the other members of the family Leiognathidae.

Leiognathus spp.: There are many species of *Leiognathus,* varying in length from 50 mm. to 200 mm. With the exception of the male *L. rivulatum* they have comparatively small luminous glands. Even when compared with *Gazza* and *Secutor,* this has a comparatively small luminous body and thick ventral cavity walls, which are only moderately translucent, thus diminishing the brightness of the luminosity.

The species *L. equulus, L. fasciatus, L. splendens, L. lineolatus, L. bindus, L. berbis, L. argenteum, L. dussumieri, L. stercorarius,* and *L. daura* are also only moderately luminous. There is an interesting feature of the Japanese species, *L. rivulatum,* viz.: the luminous gland of the male is either very large or else very small. I am of the opinion, though by no means certain, that this differ-

ence in size is due to age. The luminous gland of the female is smaller and the luminosity of the female is therefore very weak compared with that of the male.

The luminous gland of *L. rivulatum* differs from that of all other Leiognathidae in that it does not surround the oesophagus completely, but occurs as an external swelling on the dorsal part only.

L. elongatus also possesses a very small luminous gland with a poor reflector; in consequence its luminosity is feeble.

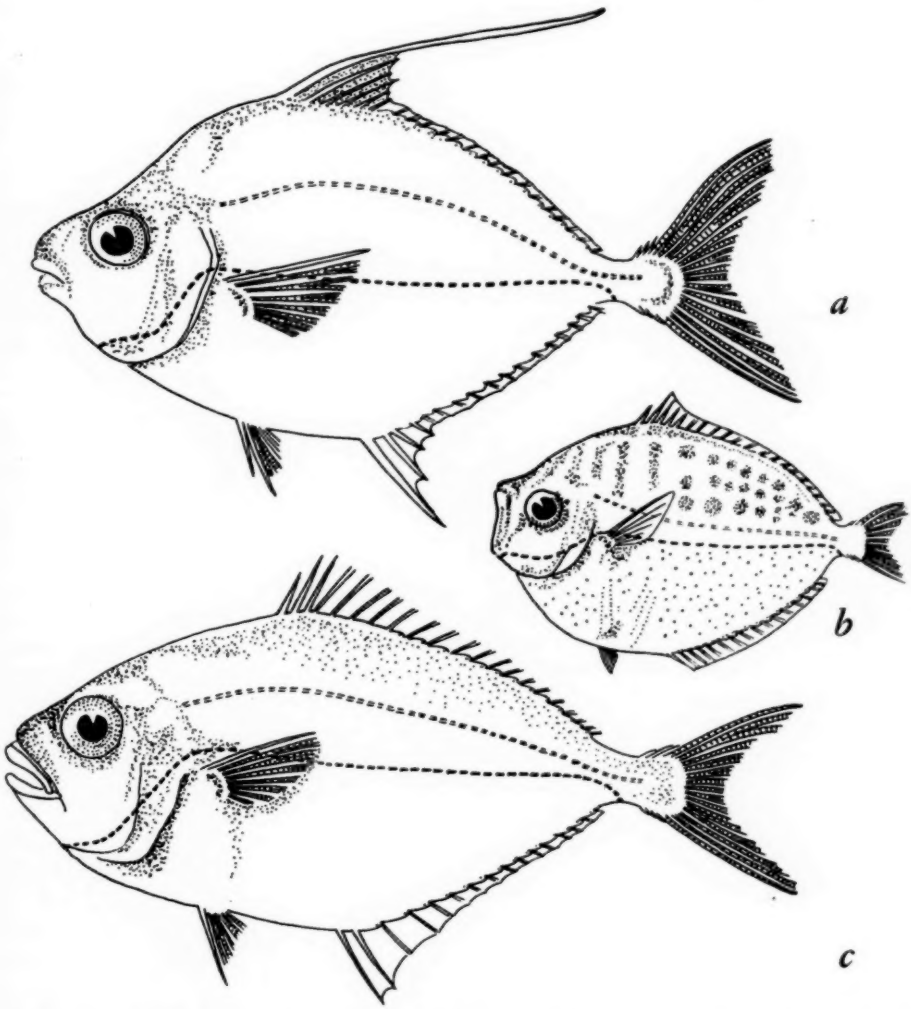

FIG. 6. *a, Leiognathus equulus* (Forsk.); *b, Secutor insidiator* (Bloch); *c, Gazza minuta* (Bloch). The luminous organs are not seen externally, so that the fish look like common non-luminous fishes, but the lower half of these fish bodies, namely, the parts below the black lines, are a lightning-like bluish-white color.

Remarks on the Luminescence

A specimen of *Gazza minuta* and one of *Secutor insidiator* were put into a tank of sea water in a dark room and their luminescence was studied. No luminescence could be seen when the fish were viewed dorsally, but if they were viewed laterally a diffuse bluish-white luminosity could be seen. If the area where the transparent scales are arranged was examined directly or obliquely from below, a faint bluish light was seen, emanating from the chest, thorax, abdomen, and tail areas. The light showed uninterruptedly in these areas. It did not shine brilliantly, but was feeble and diffused.

If the fish received a strong stimulus or was removed from the water, the lower part of the body lighted up brilliantly, most strongly in the thoracic and abdominal regions. This sudden increase in brilliancy was accompanied by a croaking sound, the production of which is a peculiarity of the Leiognathidae.

If during this brief period of maximum brilliancy the fish was enveloped in a cellophane wrapper and was laid on a photographic film, it would produce a bright image.

After death the luminous gland was surrounded by the membrane and the light was no longer visible, but if the fish was dissected and the membrane covering the gland was removed, this membrane was found to be luminous and, when kept in an ice box at 5–10° C., it remained so for 2 days.

Contents of the Luminous Gland

When the substance of the luminous gland is freshly made up as a 3 per cent salt emulsion, the whole of the emulsion will be luminescent, but if it is allowed to stand, only the upper layer exposed to the atmosphere will glow while the deeper lower layer becomes non-luminous. When shaken up in air the whole emulsion becomes luminous again.

Luminescence is greatest at a temperature of 26°–30° C. in the tropics (in Japan at about 20° C.) and becomes feeble at 4° C. When the temperature is raised, it increases and finally disappears at 45° C., but after once attaining this latter temperature it fails to recover its luminosity even when cooled again. An emulsion in nearly 3 per cent NaCl gives the best results; an emulsion in distilled water produces no light. If such a distilled-water emulsion is centrifuged the upper clear solution is non-luminous but the sediment is luminous. Microscopically this emulsion is made up of disintegrated particles of gland cells with innumerable bacteria, and it appears from the results of these experiments that the contents of the luminous gland consist of luminous bacteria. In order to test this, isolation experiments were carried out to cultivate them in a 3 per cent NaCl agar-agar culture medium.

Culture of the Luminous Bacteria

A pure culture of the luminous bacteria from the luminous glands was prepared by the usual bacteriological techniques. After 8–10 hours a small, round, transparent and luminous colony appeared. From this start a pure culture which was free from any contaminating bacteria was obtained.

It was clearly demonstrated that the same kind of fishes always had the same kind of luminous bacteria and that the Leiognathidae of the tropical sea and those of Japan possessed luminous bacteria of the same group, with only slight variations probably due to the effects of temperature. There is a curious feature, viz., the bacteria in culture are not as brilliant as are those in the gland, probably because of the unsuitability of the medium for greatest luminosity. The details of the bacteriological work will be presented elsewhere.

SUMMARY

Some luminous fishes show no outward peculiarities in structure or appearance and

resemble ordinary non-luminous fish. This is because the luminous body lies inside the fish and cannot be seen from outside.

These fishes differ from other luminous fishes by their unusually large luminous areas, which utilize as much as one half or one third of the muscles of the extremely complicated body structure of the fish.

The luminous fishes hitherto known are provided with a direct radiating luminous organ, while the fishes described in this paper possess an indirect radiating luminous organ. These organs of indirect emission are peculiar organs of a novel type, which appear to be confined to *Acropoma* species, the Leiognathidae, and *Apogon marginatus* Döderlein.

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Sea Temperatures, Hawaiian Island Area[1]

A Study of the Distribution of Ocean Temperatures in the Surface and Subsurface Layers Based upon Bathythermograph Observations

DALE F. LEIPPER AND ERNEST R. ANDERSON[2]

INTRODUCTION

SINCE 1940 the supply of available sea-temperature information has been greatly increased through the use of the bathythermograph (Spilhaus, 1940), an instrument which may be lowered from moving vessels to provide a continuous trace of temperature against depth. The temperature values are usually accurate to within ± 0.3° F. Greatest depths attained are approximately 180, 450, or 900 feet, depending upon the type of bathythermograph used. A detailed sea-temperature study of the Hawaiian Island area (the area from 15° to 30° north latitude and 150° to 165° west longitude) was prepared by the Bathythermograph Section at Scripps Institution of Oceanography (Leipper and Anderson, 1948; Hiatt, 1948). This study, made from 5,407 observations, is the basis of the summary presented here. A similar study was made in the Philippine Island area (Leipper and Wood, 1947) but has not yet been published.

Purpose of the investigation

The purpose of this investigation is threefold: (1) to show the horizontal and vertical distribution of temperature; (2) to show the amount of data that is available and how it is distributed; and (3) to further the development of a model temperature-distribution study that may in the future be used for other regions.

Availability of bathythermograph data

The file of bathythermograms for the Pacific and Indian Oceans is maintained at Scripps Institution of Oceanography, La Jolla, California, and at the U. S. Hydrographic Office, Washington, D. C. Copies of observations may be requested from the Hydrographic Office.

Acknowledgments: Clerical and statistical assistance was furnished by Misses A. Kutz, V. Wilburn, M. Hunter, M. Oakes, E. Trowbridge, and Mrs. B. Rimbach. Drafting was done by Mrs. M. Robinson and photographic work by Mr. P. Williams.

DISTRIBUTION OF BATHYTHERMOGRAMS

The bathythermograph observations used for this investigation cover the period from January, 1941, to November, 1947. Of the bathythermograms available, 5,377 were suitable for use.

The time distribution of the bathythermograms is shown by Tables 1, 2, and 3 following the text. Table 1 shows the yearly percentage distribution; Table 2, the total monthly percentage distribution; and Table 3, the monthly percentage distribution in different years. The space distribution of the bathythermograms is shown in Figure 1. (Figures appear at the end of the text and tabular material begins on page 232.)

[1]Contributions from the Scripps Institution of Oceanography, University of California, New Series No. 468. This work represents results of research carried out by the University of California, under contract with the Office of Naval Research and the Hydrographic Office of the Department of the Navy.

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Two groups of cruises, designated as the *H* and *Q* cruises, were made near the entrance to Pearl Harbor during 1944 and the early part of 1945. The following tabulation shows the dates of these cruises as well as the number of bathythermograph observations taken.

H AND *Q* CRUISE DATA

CRUISE	DATE	NUMBER OF BATHY-THERMOGRAMS
Q-1	2/24/44– 3/29/44	60
Q-2	3/29/44– 4/22/44	60
Q-3	4/23/44– 5/14/44	60
Q-4	5/15/44– 6/26/44	60
Q-5	6/27/44– 9/ 4/44	60
Q-6	9/15/44–11/13/44	60
Q-7	11/14/44– 2/12/45	60
Q-8	2/12/45– 2/20/45	7
H-1	3/13/44– 3/29/44	42
H-2	3/29/44– 4/17/44	56
H-3	4/17/44– 5/ 6/44	57
H-4	5/ 6/44– 5/30/44	60
H-5	6/ 1/44–10/ 9/44	108
H-6	11/16/44– 2/20/45	63

HORIZONTAL TEMPERATURE DISTRIBUTION

Horizontal temperature distribution based on averages by 1-degree quadrangles of latitude and longitude

The horizontal distribution of average temperature at the surface and at depths of 100 feet, 200 feet, and 300 feet is shown in Figures 2 to 13 for each of the 12 months of the year. March and September average temperatures were, respectively, lowest and highest of the year. June and December were months having temperature distributions typical of months of transition.

In preparing the monthly average temperature charts, the following procedure was used: At each depth level, all available temperatures for each 1–degree quadrangle were averaged by months. To obtain time continuity, the monthly averages for each quadrangle where there were sufficient data were plotted against time, and a curve, smoothed visually, was drawn through the points. Monthly average temperatures were then read from this smoothed curve. The values for each month were plotted on a map by position, and the isotherms were drawn.

The ocean current systems which are present affect the horizontal temperature distribution. In March the southern portion of the Hawaiian Island area is under the influence of the northeast trade winds with a resulting ocean current toward the west known as the North Equatorial Current. In the northerly portion of the area the North Pacific Current flows toward the southeast. Between these two currents as shown in Figure 14 is a region where the flow is variable (Sverdrup, Johnson, and Fleming, 1946: 723, appendix, Chart VII). This region coincides with the region where the pattern of isotherms is most irregular, as shown in Figures 2 to 13.

The extremes of average temperature

For each month of the year, at particular depths, the maximum average monthly temperature occurring in any 1-degree quadrangle of the Hawaiian Island area was selected. Similarly, the minimum average was obtained. These, together with the differences between them, are presented in Table 4 at several depths for each month. At the surface and at 100 feet, the differences are smaller during the summer than during the winter. At 200 and 300 feet, the differences appear to be almost constant.

Table 5 (page 233) shows results of analysis of the smoothed annual temperature-variation curves which were drawn for each 1-degree quadrangle as explained earlier. An examination of the table shows that the minimum occurred the greatest percentage of the time in March at all levels except 300 feet; and the maximum, in September at all levels except 300 feet. At 300 feet the minimum occurred most often in April and the maximum most often in October.

Figures 16 and 17 present the maximum and minimum monthly average temperatures, respectively, for the surface and the 100-,

200-, and 300-foot levels. To obtain Figure 16, the highest monthly average temperature at each depth in each quadrangle was plotted, regardless of the month or year in which it occurred, and isotherms were drawn. Figure 17 was prepared similarly for lowest monthly average temperatures.

The highest single surface temperature recorded in the Hawaiian Island area was 90° F. at 19° N and 157° W in August, 1942, while the lowest single temperature recorded was 60.9° F. at 28° N and 163° W in January, 1947.

Annual sea temperatures at a depth of 400 feet

As is apparent in Figures 22 and 27, sea temperatures at a depth of 400 feet have only a small annual variation. Values for all months of the year have therefore been averaged together by 1-degree quadrangles to obtain the annual average. These annual averages were plotted by position and isotherms drawn (see Figure 15). This figure, when compared with Figures 22 and 27, indicates that at 400 feet the variation of sea temperature with position greatly exceeds the variation with time.

Comparison of average temperatures in different years

Figure 18 compares the annual variation of temperature at the surface, 100 feet, 200 feet, and 300 feet for each of the years 1943 to 1947 with the average annual variation for all years combined. There is considerable difference between the curves representing different years. The year 1943 was warmer than average at the surface and 100 feet. Not enough data were available to show the deviation at 200 feet and at 300 feet in this year. The year 1944 was virtually an average year at the upper two levels, while at the two lower levels there was some variation from the average. The year 1945 was definitely a warmer-than-average year in the upper two levels, while in the lower two it was generally warmer with a few months colder than average. The first part of the year 1946 was definitely warmer than average, while the latter part of the year was colder than average at all levels. The year 1947 was a colder-than-average year at all levels with the deviation being the greatest in the upper 100 feet.

Average temperature in the vicinity of Oahu

Figure 19 shows the temperature distribution in the vicinity of Oahu for the surface, 100 feet, 200 feet, and 300 feet. The isotherms at each depth are based upon averages computed for each 10-minute quadrangle of latitude and longitude. Thus the details of the average temperature distribution near Oahu are shown. In this region many observations are available and detailed information may have practical value.

VERTICAL TEMPERATURE DISTRIBUTION

Southwest-northeast cross section

Figures 20 and 21 present average southwest-northeast temperature-depth sections for winter and summer months, respectively. All available bathythermograms for the two periods of time, and within the band denoted in Figure 1, were used to obtain the averages at various positions and depths. These averages form the basis of the sections.

Monthly average temperature-depth curves

Figure 22 shows curves through the average temperatures at different depths for a 5-degree quadrangle covering the area 20° to 25° N and 155° to 160° W. These curves were obtained by averaging all available temperatures for each month at 10-foot depth intervals down to 100 feet and at 25-foot intervals down to 425 feet, plotting these averages against depth, and joining the points. Such curves do not show the typical temperature-depth structure because of smoothing which occurs in averaging. The number of temperatures included in the average is shown beside each point.

Figure 23 shows the average temperature-depth curves for two specific points. The curves labeled "H" are taken from *H* cruise data. These cruises consisted of 386 bathythermograph observations from March, 1944, to February, 1945. All data were collected at 21° 18′ N and 157° 53′ W, approximately 0.75 mile south southwest of Honolulu in 100 feet of water. These data were averaged together by months with the results as shown in the figure. The curves labeled "Q" are taken from *Q* cruise data. These cruises consisted of 427 bathythermograms from February, 1944, to February, 1945. The station was located at 21° 18′ N and 157° 58′ W about 1.75 miles due south of the entrance to Pearl Harbor in about 600 feet of water.

These two stations are located approximately 5 miles apart, and the data were taken during the same year. It is interesting to note that during the months of March and April the average curves were identical, but during the other months the *H* cruise data showed appreciably lower temperature at all depths.

Typical bathythermograms

Figure 24 contains copies of actual bathythermograms selected as typical of a northern and a southern portion of the area under study for the months of March, June, September, and December. These single records show several prominent features which are not apparent in curves drawn through average temperatures at selected depths. One of these features is the deep layer of nearly isothermal water which is present on several of the individual curves. Another is the strong thermocline. Each of these characteristics is typical of nearly all individual bathythermograms in this area but the process of averaging and the decreasing frequency of temperature readings with depth causes them to disappear from the average temperature-depth curves. Thus it is desirable to consider typical single observations as well as average curves.

Depth of the virtually isothermal layer

The average depth of the virtually isothermal layer for summer and winter periods is shown in Figure 25. The charts were prepared by reading from the bathythermograms the layer depth to the nearest foot and averaging the results by 1-degree quadrangles. These data were then plotted, and isolines of depth were drawn. The virtually isothermal layer is, on the average, deeper than the 180-foot maximum depth for the "shallow" bathythermograph; hence, the "deep" bathythermographs are the only ones that reach the thermocline. As a result, only 40 per cent of the total number of bathythermograms available for this study were used in establishing the layer depth. Two conclusions may be drawn from Figure 25: the layer depth varies considerably with position; and during the winter the depth is greater than during the summer.

An attempt was made to draw layer-depth charts for each month of the year. Although many observations were available, the variability within any given month and any given quadrangle was so great that it was not possible to draw isolines that exhibited good continuity.

Diurnal and annual variation of temperature

In August, 1941, the U.S.S. "Pyro" took bathythermograph observations every hour in the area 21° to 34° N and 138° to 157° W. These data were analyzed by H. U. Sverdrup and others to determine the diurnal variation of temperature. Figure 26 shows the results of this analysis.

The wind-stirred layer at the time of these observations was approximately 120 feet thick with 75° F. as the average temperature of the layer. Between the surface and 120 feet the temperatures were read at 30-foot intervals. The temperature differences between 120 feet and each other level were determined and plotted. The figure shows that the upper layer is nearly isothermal during the early

morning, but that the vertical gradient increases as the effect of solar radiation is felt. The time of maximum temperature occurs later at greater depths because time is required for heat to reach these depths by conduction.

The annual variation of temperature at subsurface depths in the area 20° to 25° N and 157° to 160° W is shown in Figure 27. The maximum temperature occurs at 400 feet approximately 1.3 months later than at the surface. A secondary maximum is indicated in January. The maximum shown at 400-foot level in April is probably not a real feature but one due to the uneven frequency distribution of observations.

ADDITIONAL DATA AVAILABLE

In addition to what has been published here, certain further investigations have been made and results are available from the Scripps Institution of Oceanography. Among these results are charts of the distribution of observations by months and hydrographic station data.

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TABLES

TABLE 1
DISTRIBUTION OF BATHYTHERMOGRAMS BY YEARS

YEAR	PERCENTAGE
1941	3.2
1942	2.5
1943	16.0
1944	43.0
1945	15.1
1946	11.7
1947	8.6

TABLE 2
DISTRIBUTION OF BATHYTHERMOGRAMS BY MONTHS

MONTH	PERCENTAGE
January	7.1
February	10.0
March	10.4
April	11.8
May	9.9
June	6.8
July	7.2
August	9.9
September	9.2
October	6.4
November	6.3
December	4.9

TABLE 3

DISTRIBUTION OF BATHYTHERMOGRAMS BY MONTHS IN DIFFERENT YEARS
(All figures are given as percentages.)

MONTH	1941	1942	1943	1944	1945	1946	1947
January	0.0	0.0	0.3	5.8	23.4	2.1	7.0
February	1.2	13.4	18.4	7.3	13.6	7.0	7.8
March	5.3	0.0	13.0	8.7	9.4	1.7	30.0
April	0.0	11.2	13.2	12.0	10.2	9.2	15.9
May	2.4	22.4	9.5	14.1	2.8	2.9	11.3
June	1.8	11.9	1.8	7.8	3.4	5.1	17.6
July	3.5	0.0	5.0	7.2	6.9	9.1	10.4
August	42.9	14.9	3.6	10.3	8.3	16.7	0.0
September	2.9	9.7	12.1	8.0	6.3	20.5	0.0
October	10.6	0.0	7.0	7.0	3.8	11.0	0.0
November	24.7	0.0	5.0	6.6	5.4	8.7	0.0
December	5.3	16.4	11.0	5.3	6.4	5.9	0.0

TABLE 4

MAXIMUM AND MINIMUM MONTHLY AVERAGE TEMPERATURES AT DIFFERENT DEPTHS

	MAXIMUM				MINIMUM				DIFFERENCE			
Depth in feet	0	100	200	300	0	100	200	300	0	100	200	300
January	80	79	78	78	68	68	66	64	12	11	12	14
February	79	78	78	77	67	66	65	64	12	12	13	13
March	78	77	77	76	66	67	64	64	12	10	13	12
April	78	77	77	76	68	68	64	64	10	9	13	12
May	79	78	78	77	70	69	66	64	9	9	12	13
June	80	80	79	77	74	71	68	64	6	9	11	13
July	82	80	80	78	76	73	66	64	6	7	14	14
August	82	81	81	79	77	75	68	66	5	6	13	13
September	82	82	81	80	77	76	67	67	5	6	14	13
October	82	82	82	80	76	75	68	66	6	7	14	14
November	82	81	81	80	72	72	68	67	10	9	13	13
December	80	80	80	79	70	70	67	66	10	10	13	13

TABLE 5

MONTHS IN WHICH MAXIMUM AND MINIMUM TEMPERATURES OCCURRED MOST OFTEN ON SMOOTHED ANNUAL VARIATION CURVES WHICH WERE DRAWN FOR EACH 1-DEGREE QUADRANGLE

MINIMUM			MAXIMUM		
Depth	Month	Frequency	Depth	Month	Frequency
Feet		*Per cent*	*Feet*		*Per cent*
Surface	March	56.4	Surface	September	64.5
100	March	57.9	100	September	71.0
200	March	46.6	200	September	51.1
300	April	39.0	300	October	40.7
All	March	48.9	All	September	54.9

FIGURES

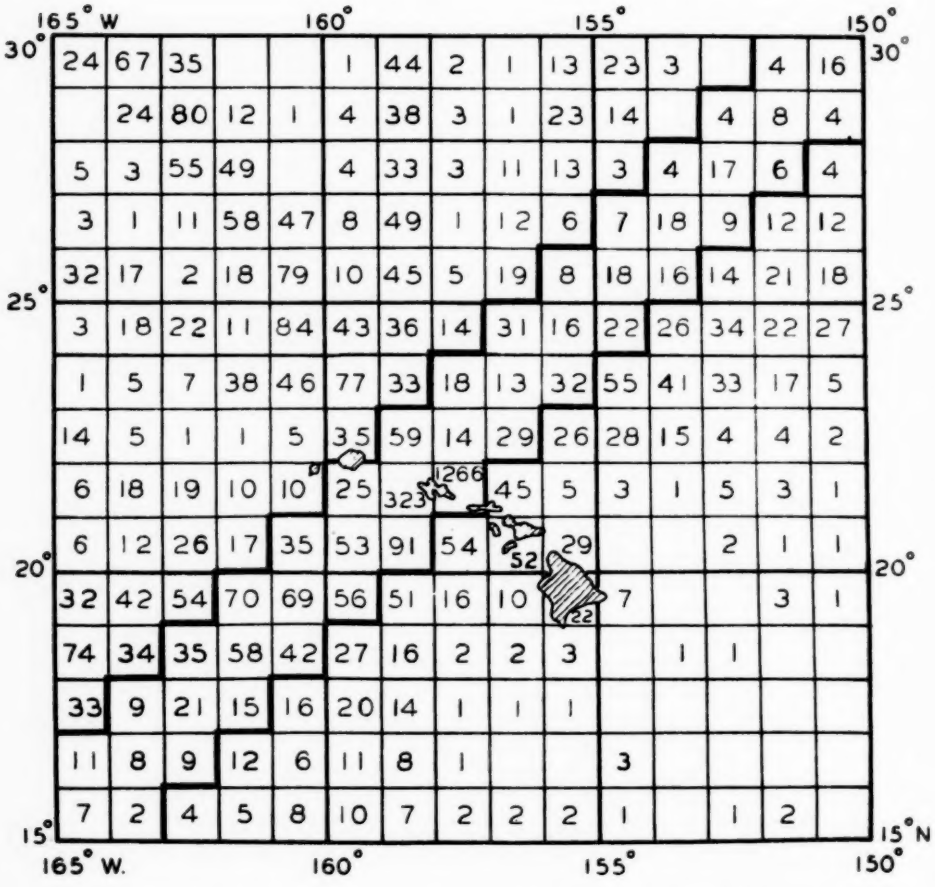

FIG. 1. Distribution of bathythermograph observations processed prior to November, 1947.

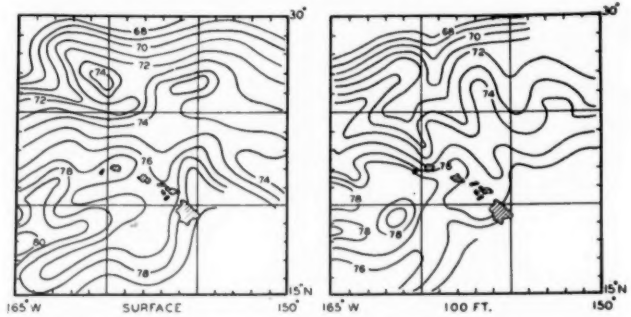

FIG. 2. JANUARY, average sea temperatures (° F.) at selected depths (1941–1947).

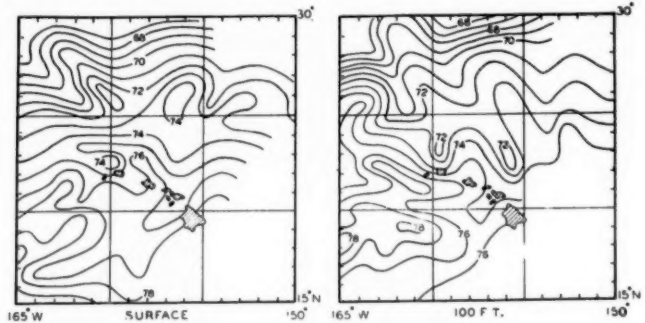

FIG. 3. FEBRUARY, average sea temperatures (° F.) at selected depths (1941–1947).

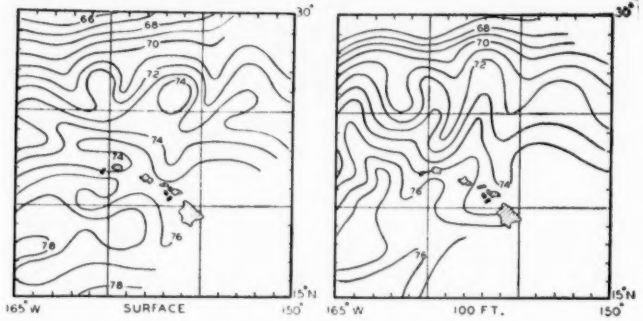

FIG. 4. MARCH, average sea temperatures (° F.) at selected depths (1941–1947).

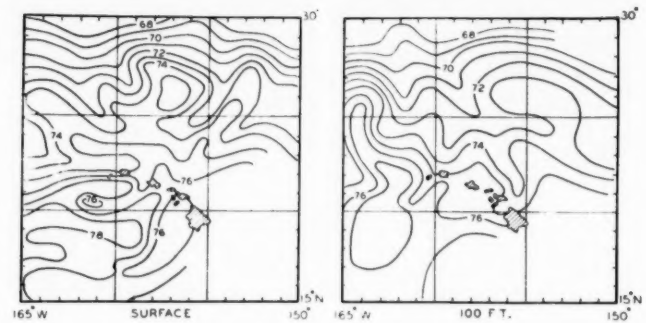

FIG. 5. APRIL, average sea temperatures (° F.) at selected depths (1941–1947).

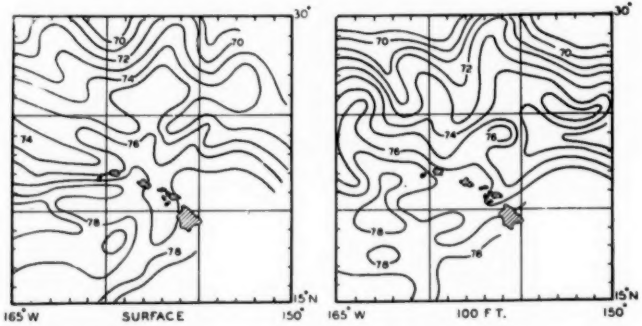

FIG. 6. MAY, average sea temperatures (° F.) at selected depths (1941–1947)

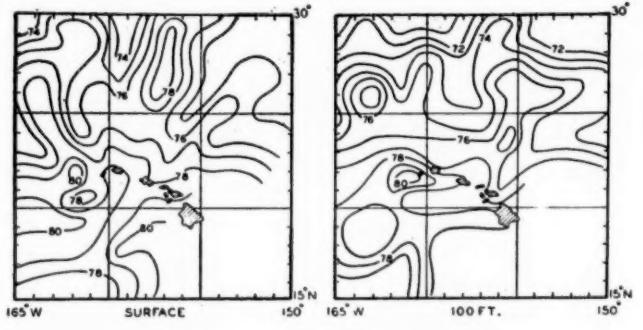

FIG. 7. JUNE, average sea temperatures (° F.) at selected depths (1941–1947).

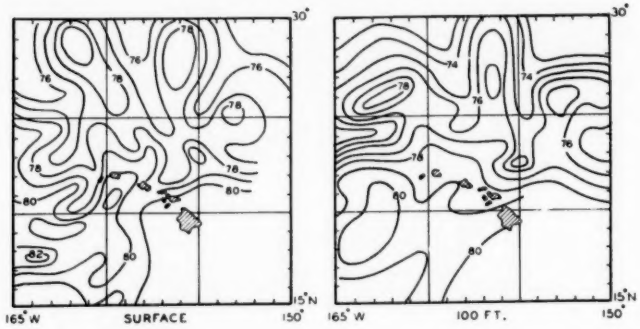

FIG. 8. JULY, average sea temperatures (° F.) at selected depths (1941–1947).

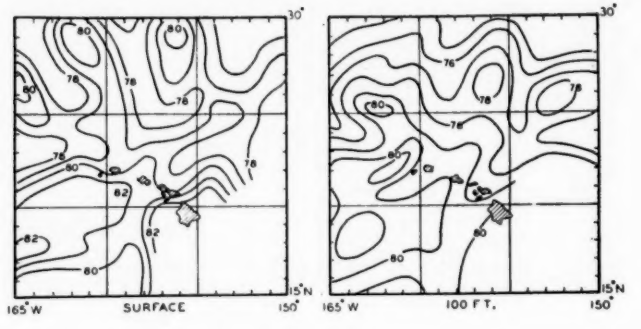

FIG. 9. AUGUST, average sea temperatures (° F.) at selected depths (1941–1947).

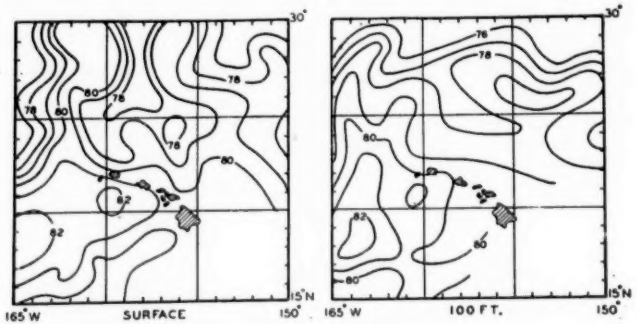

FIG. 10. SEPTEMBER, average sea temperatures (° F.) at selected depths (1941–1947).

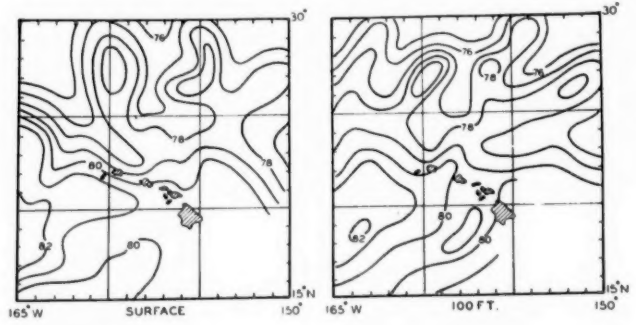

FIG. 11. OCTOBER, average sea temperatures (° F.) at selected depths (1941–1947).

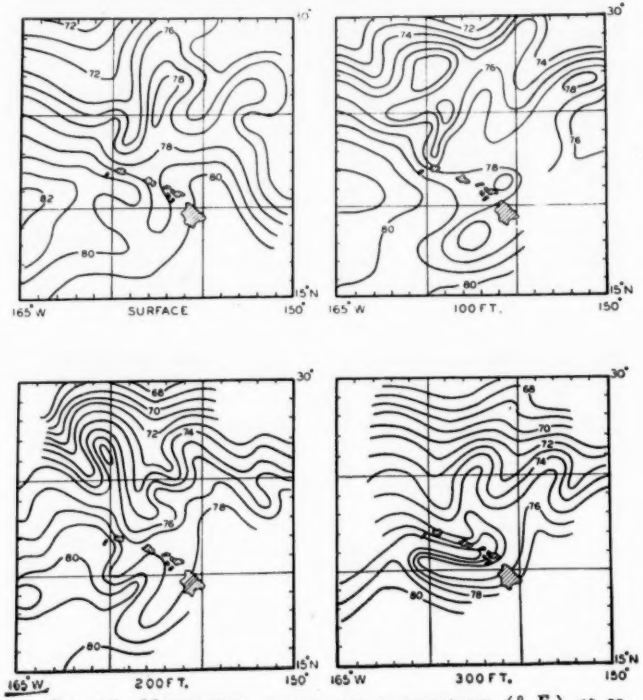

FIG. 12. NOVEMBER, average sea temperatures (° F.) at selected depths (1941–1947).

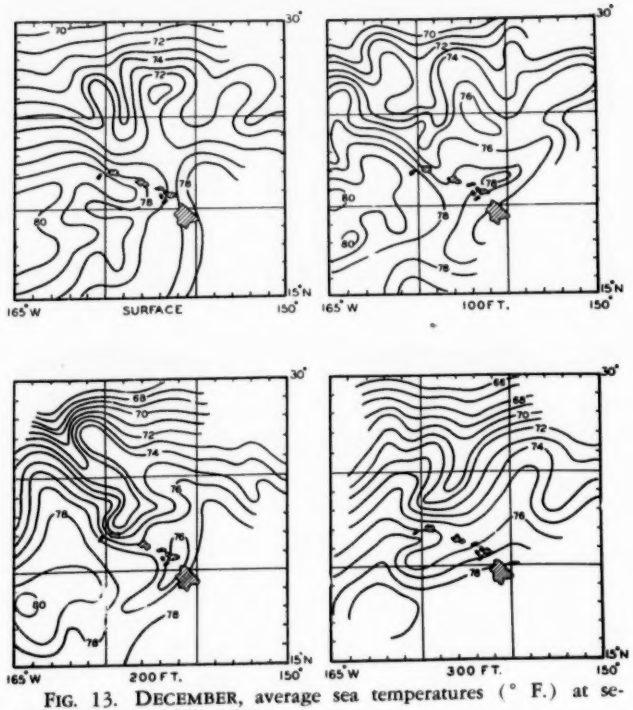

FIG. 13. DECEMBER, average sea temperatures (° F.) at selected depths (1941–1947).

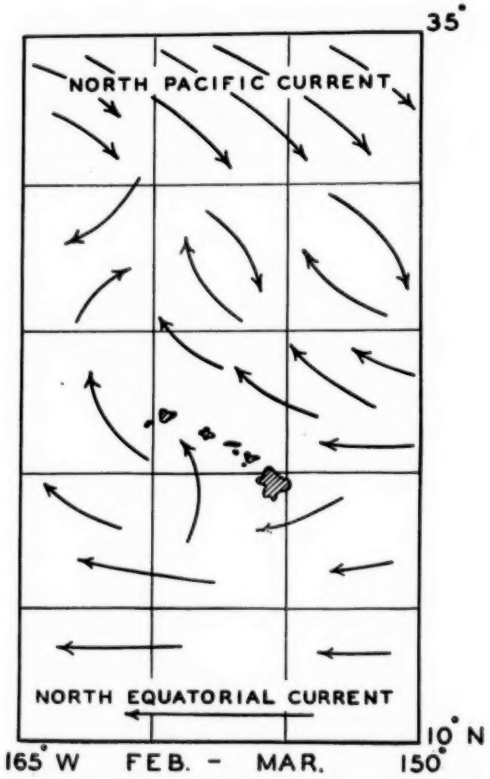

FIG. 14. Sketch of ocean currents; after Sverdrup.

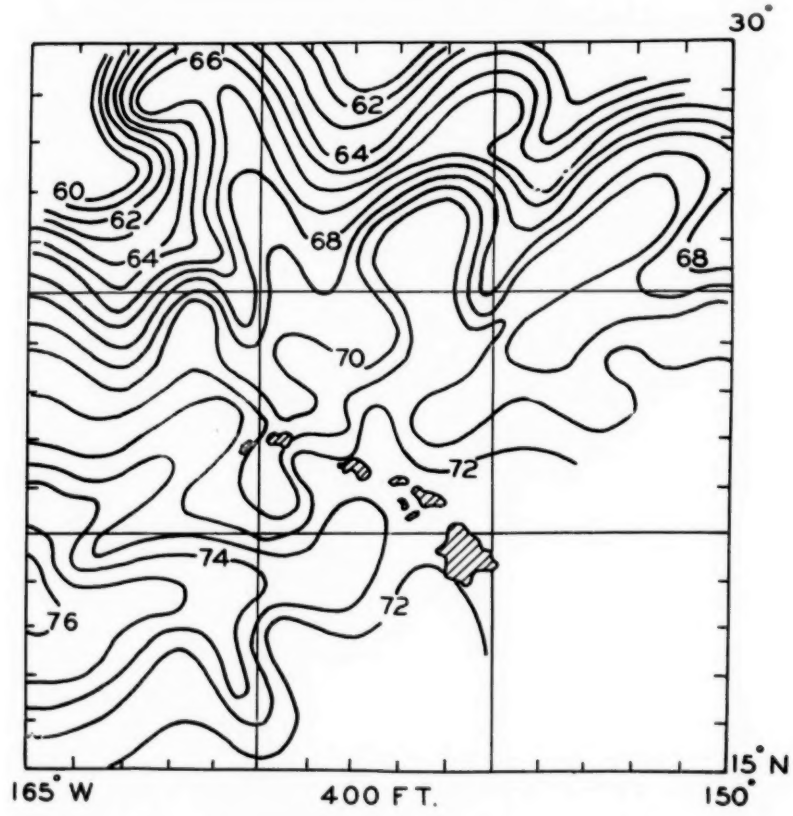

FIG. 15. Annual average sea temperatures (° F.) at 400 feet.

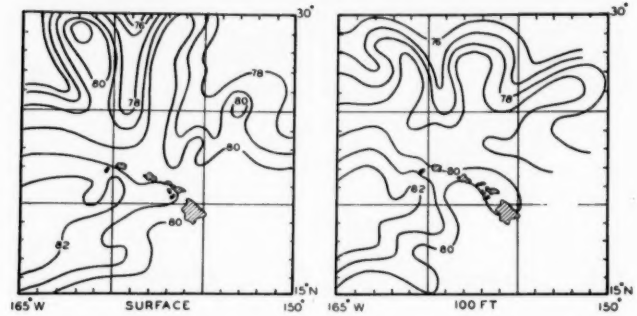

FIG. 16. Maximum monthly average sea temperatures (° F.), (1941–1947).

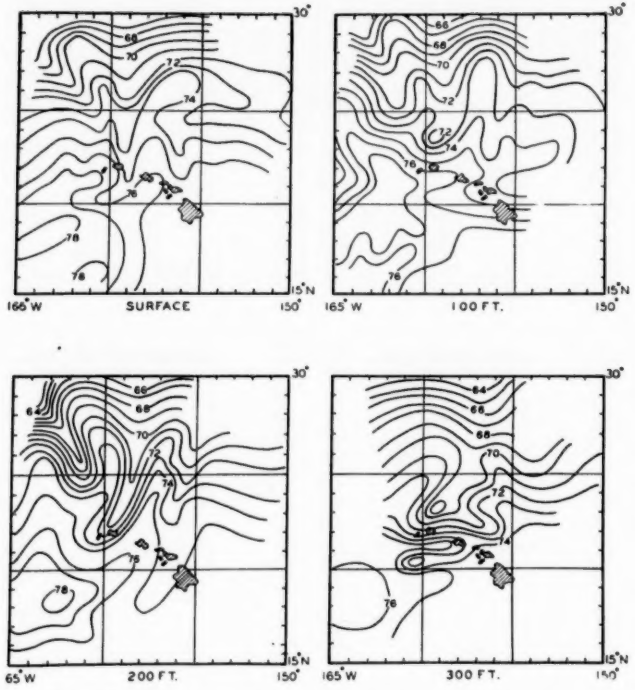

FIG. 17. Minimum monthly average sea temperatures (° F.), (1941–1947).

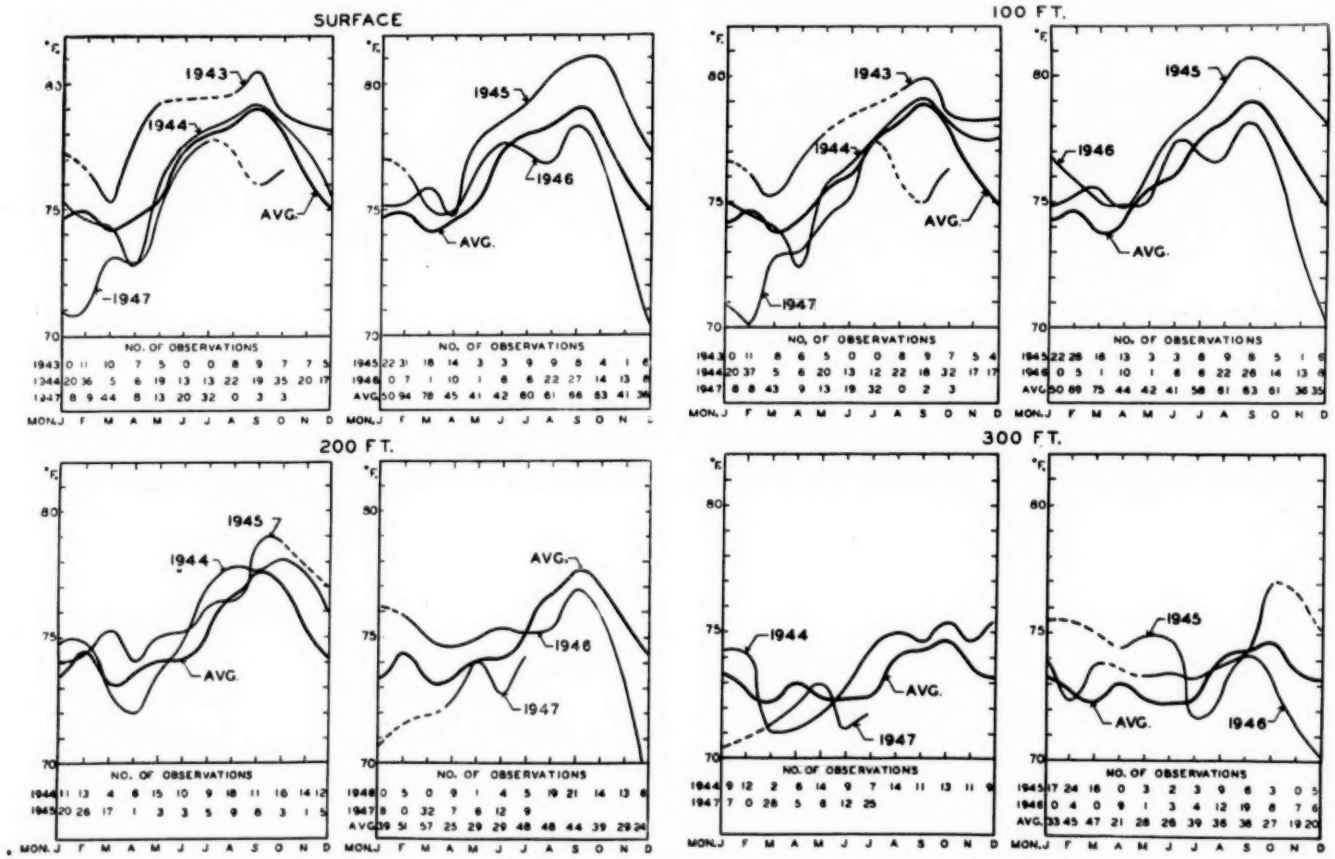

FIG. 18. Annual sea temperature variation (° F.) shown by curves through monthly averages (1943–1947), 20°–25° N, 155°–160° W.

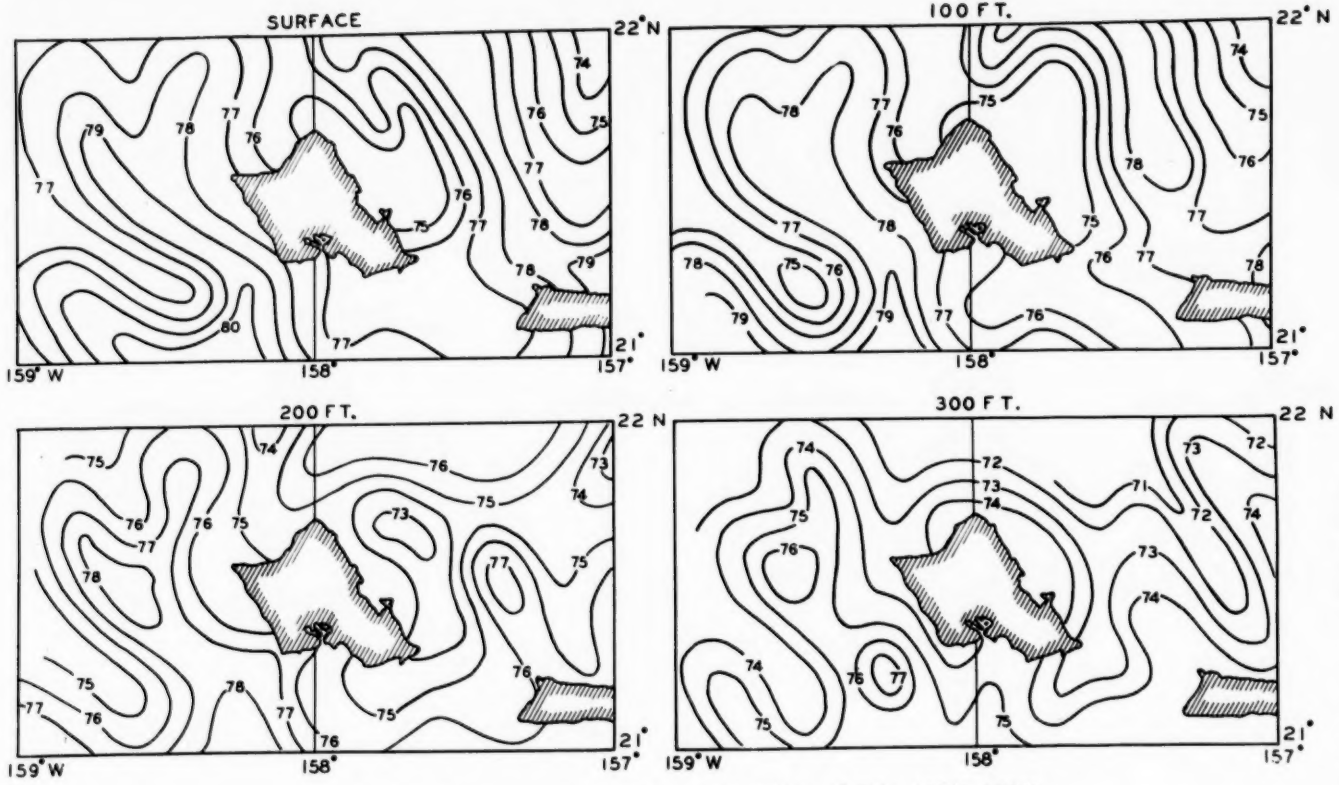

FIG. 19. Annual sea temperatures (° F.) in the vicinity of Oahu (1941–1947).

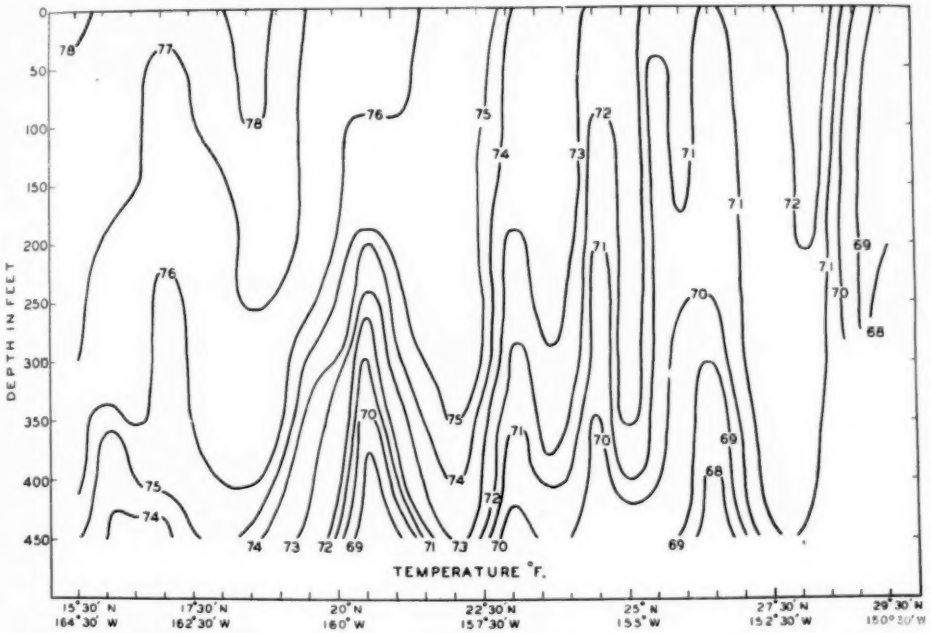

FIG. 20. SW–NE sea temperatures (° F.). Cross section (January, February, March, 1941–1947).

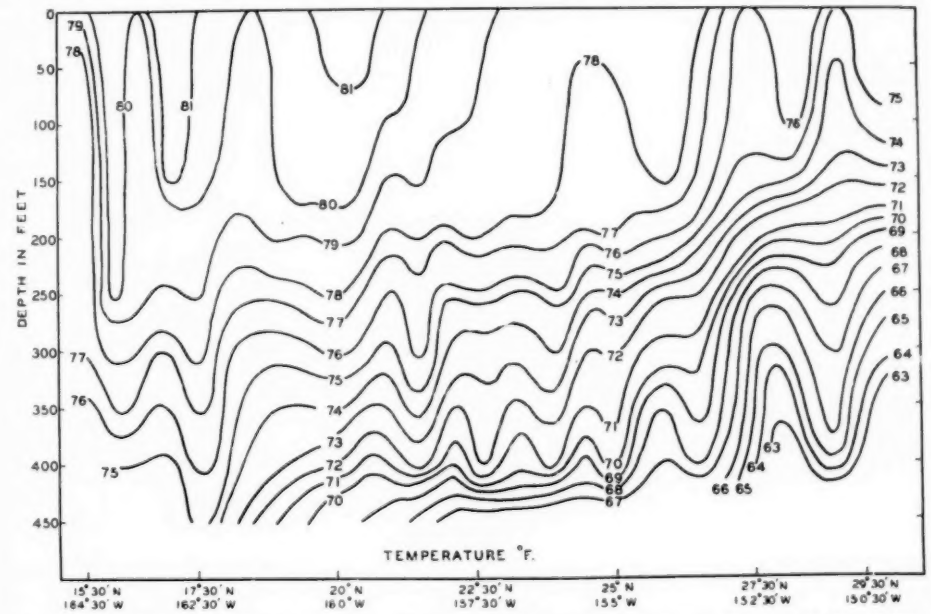

FIG. 21. SW–NE sea temperatures (° F.). Cross section (August, September, October, 1941–1947).

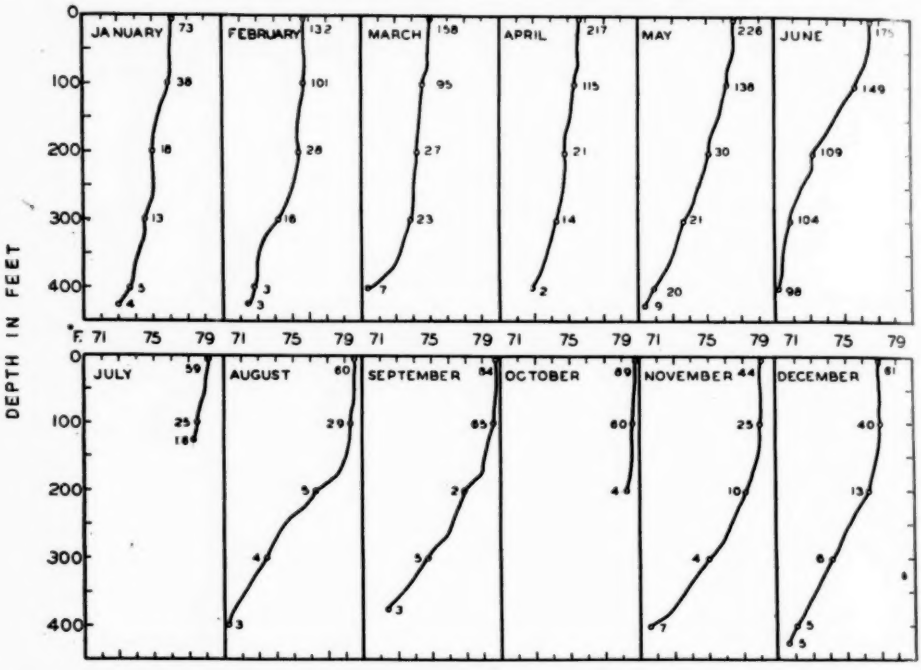

FIG. 22. Temperature depth curves; monthly averages (1941–1947); 20°–25° N, 155°–160° W.

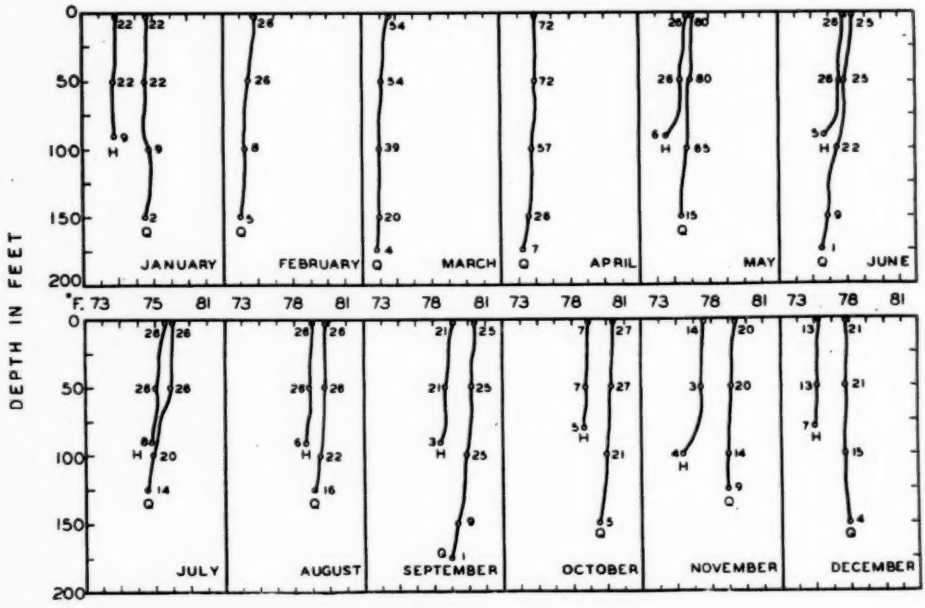

FIG. 23. Temperature depth curves; monthly averages. *H* cruises: March, 1944–February, 1945; 21° 18′ N–157° 53′ W. *Q* cruises: February, 1944–February, 1945; 21° 18′ N–157° 53′ W.

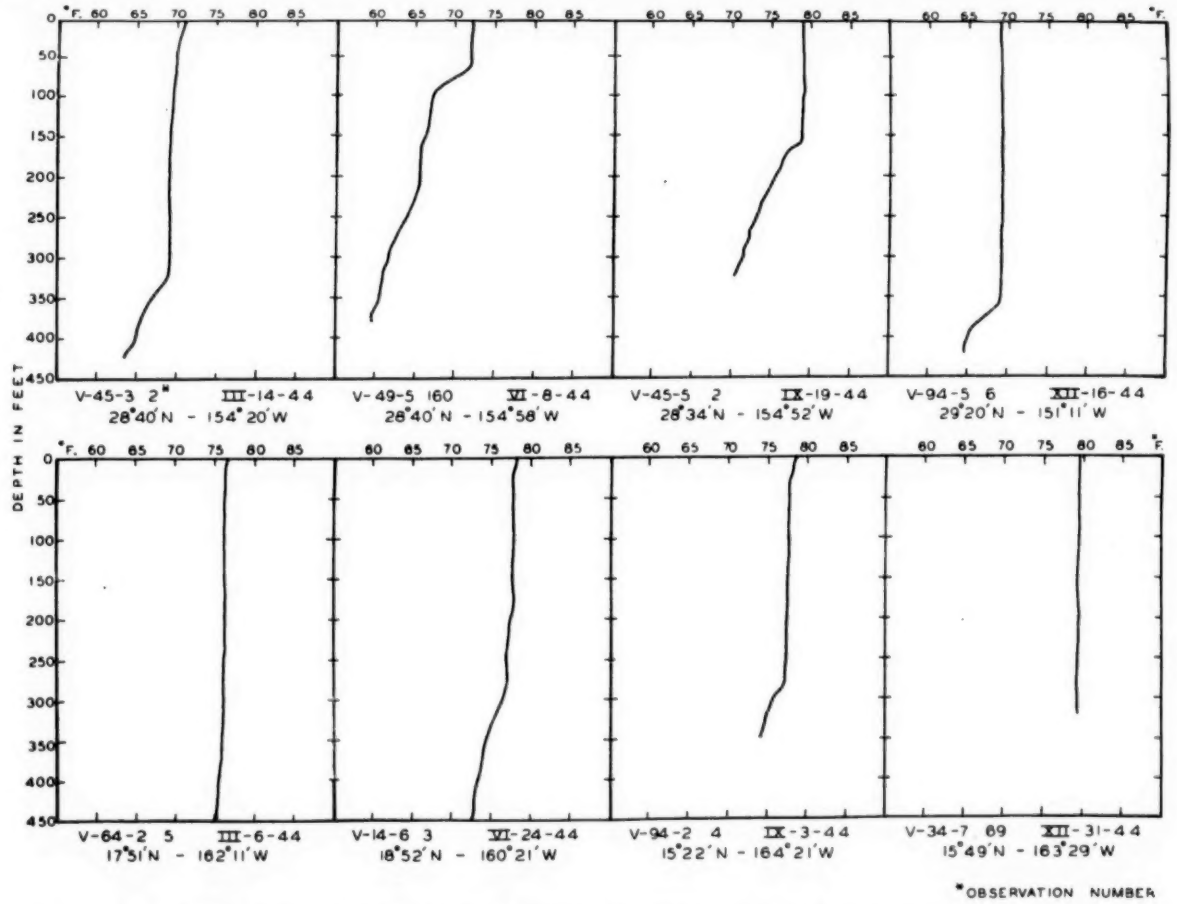

FIG. 24. Typical bathythermograms for March, June, September, December. Upper row, northern portion. Lower row, southern portion.

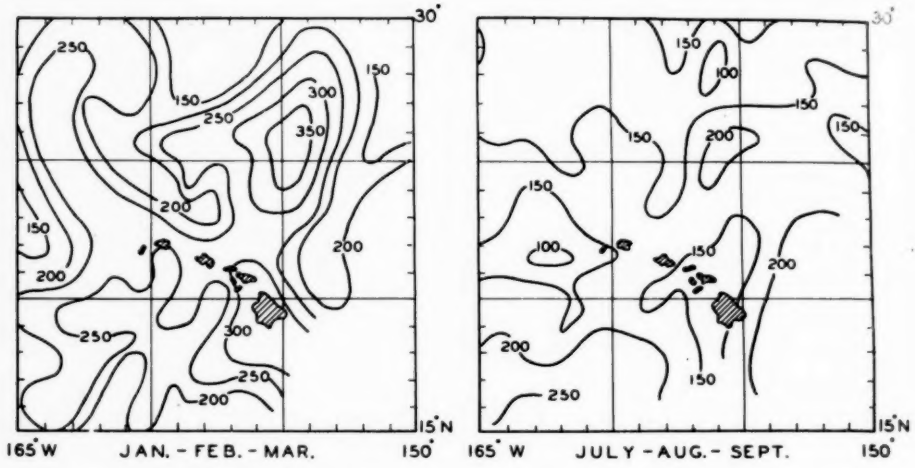

FIG. 25. Average depth of the virtually isothermal layer (1941–1947).

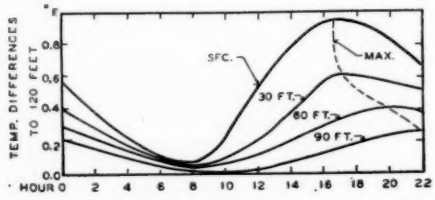

FIG. 26. Diurnal sea temperature variation (° F.); 21°–34° N, 138°–157° W.

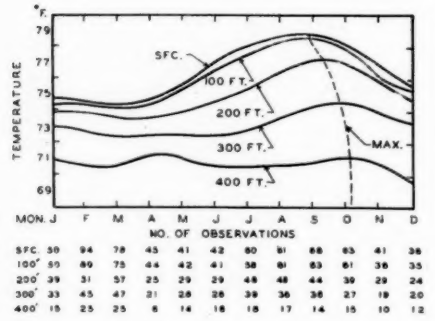

FIG. 27. Annual variation of temperature. 20°–25° N, 157°–160° W.

A Taxonomic Revision of the Hawaiian Species of the Genus *Carex*[1]

ROBERT W. KRAUSS[2]

INTRODUCTION

LINNAEUS PUBLISHED the genus *Carex* in *Genera Plantarum,* Ed. 1, p. 280, 1737, and again in *Genera Plantarum,* Ed. 5, p. 420, 1754. The present use of the name is based on the latter. The type species for the genus has been designated by Mackenzie (1923: 343) as *Carex acuta* var. *nigra* L., which has been known erroneously for some time as *Carex Goodenowii* J. Gay. Hitchcock and Green, however, have listed *Carex hirta* L. in their list of Linnaean lectotypes (Camp, 1947: 114). The problem of typification is still an open one. The genus was recognized as a natural group even before the time of Linnaeus, but from 1754 to 1915 the group was included in different genera in accordance with various generic concepts, and also attempts were made to split the genus into segregates. Since 1754 a total of 55 generic names has been proposed for the genus or its segregates. Nevertheless, it is the consensus of present-day workers that the group, though large, deserves the unity of single generic rank.

In the Hawaiian Islands specimens of *Carex* have been regularly collected by botanists visiting the islands. The earliest collection examined for this study is that of James Macrae, which was secured on the island of Hawaii during the visit of H.M.S. "Blonde" in 1825. Since that date collections have been deposited in all the major herbaria in the world. In spite of the splendid collections which are available (approximately 600 numbers were received for this study), no monographic study of the Hawaiian carices has been made. From time to time species and varieties have been described from these islands, but often by botanists working far from Hawaii and who were using not only single specimens but often mere fragments of a plant.

Taxonomic differentiation within the genus rests fundamentally on the morphological differences in the achene and surrounding perigynium. The wide and distinct variation of these structures in such a vast number of species is remarkable. Identification of the species could be effected by reference to these structures alone. However, generic groupings which included species with similar perigynia but based on other characters—primarily on the arrangement of spikes and inflorescences—have been made. The use of such characters is indispensable in breaking the genus into smaller groups but the characters show much intergradation, and their use results in the placing together of seemingly unrelated species so that doubt is cast on their being natural groupings.

In applying the characters needed to delineate the Hawaiian species, certain considerations involving the nature of species and criteria for their erection or retention in the generic population represented in the islands must be discussed. The genus *Carex,* like many other genera, has been subjected both to extreme division into species and to conservative grouping in large polymorphic or perhaps aggregate species. An investigation to determine which treatment is nearer the truth is not the purpose of this study. The recent development of experimental methods

[1]A condensation of a research problem submitted in partial fulfillment of the requirements for the Master of Science degree at the University of Hawaii in the Department of Botany, June, 1949.

[2]Department of Botany, University of Hawaii. Manuscript received June 20, 1949.

in taxonomy is adding much valuable information to the field. No worker can afford to ignore this work. However, taxonomy has not yet reached a stage where these methods can be applied to all new populations coming into the ken of the scientist, though surely all added experimental work, both in genetics and ecology, will aid the taxonomist in interpreting the morphological differences he finds.

To evaluate a population and make it intelligible to other workers, a summary of definitions of the specific and subspecific categories is in order. The following definitions merely indicate the difficulty of determining the genotype of a specimen or population from the phenotype with which the taxonomist works.

Biotypes are relatively slight morphological variations within a constant genotype which vary at random and which reflect no differences in the genetic constitution of the plant. Almost every individual could be classed as a biotype.

Forms are groups of biotypes distinct from the other biotypes of similar genetic structure by one or more very slight morphological characters which are either determined or probable responses to a peculiar environment and may or may not indicate minor genetic differences.

Varieties are groups of biotypes or forms morphologically distinct from the normal biotypic range of the population, these variations being brought about by slight genetic differences and often subsequent isolation. Varieties in a population may interbreed on contact and show a degree of intergradation in morphological characters in some of the individuals.

Species are populations of one or more varieties, forms, and biotypes which are clearly distinct morphologically from all other related populations as a result of major genic differences. Interbreeding is usually restricted or impossible between related species though certainly radical genetic morphological differences may occur in isolated species without loss of the ability to interbreed.

It is in no way intended to suggest that the above criteria are precise. In applying them to the populations of Hawaiian *Carex* it soon became apparent that both the biotypic and formal variation were much greater than has normally been allowed for species of this genus. In the case of *Carex wahuensis*, particularly, a tabulation technique was used giving all the possible visible or measurable characters by which species could be differentiated. Twenty of the most reliable characters used to differentiate *Carex* species were recorded for each of the specimens examined. The tabulation showed clearly that, in what at first appeared to be several distinct species, the gradations between supposedly distinct characters were so complete as to make impossible a delineation of more than one species. Only two minor characters in the perigynia (and these showing transitions with the typical) were found to be strong enough to be interpreted as of varietal worth. It is probable that even an able taxonomist confronted with a restricted number of specimens would have named several new species from among this group of specimens.

Examination of the work of Mackenzie on the North American carices has made very clear the seriousness of dividing into species populations which are little more than biotypes. An effort has been made here to be somewhat conservative in the erection and retention of species. In defense of this approach it may be said that the evidence strongly suggests extreme polymorphism in many of the groups. Though the species growing in the Hawaiian Islands may be distinct, the world population has other species of very close affinities to almost every one of them. These affinities are indicated in the discussion following each description. Not only does the very size of the genus suggest an extremely unstable and rapidly ramifying

genic structure, but the variations encountered in every species examined (see illustrations) have been considerable—not only in different individuals but in different sections of the inflorescence of the same individual. An effort has been made to keep intact the groups which form natural units, even though there is considerable variation within them.

Acknowledgments: Appreciation is due Dr. Harold St. John, Chairman of the Department of Botany, University of Hawaii, for guidance during the investigation. Miss Inger Achten is responsible for most of the illustrations, which add much to the usefulness of the work. I also wish to thank the directors of the various herbaria who lent material for the study. The cooperating institutions are listed under the Taxonomic Treatment. The effectiveness of the study is to a great degree the result of the work of many collectors.

DISTRIBUTION PATTERNS

The distribution of the genus is world-wide and the range of many species includes several continents. Not only have a vast number of species evolved in the genus but these species have become adapted to a very wide range in habitat as well. The majority are found in areas of more than average moisture but many survive in regions with sufficient rainfall to support grassland vegetation only. Certain of the Hawaiian carices do well in both wet forest and dry grassland, i.e., *Carex macloviana* D'Urv. and *Carex wahuensis* var. *rubiginosa* R. Krauss. Others in the islands are restricted to limited habitats; *Carex montis-eeka* Hillebd. and *Carex kauaiensis* R. Krauss are strictly high-bog plants.

Local distribution of the species and varieties is illustrated in the maps. The discussion following the species description gives the probable affinity and region of origin for each. In as many cases as possible the plants were compared with specimens collected in the type locality in other parts of the world. The following tabulation indicates the geographic affinities of the Hawaiian species.

Japan and East Asia
- *Carex Meyenii* Nees—Hawaiian endemic
- *Carex wahuensis* var. *Meyeri* Franch. and Sav. (the type variety)—Hawaiian endemic
- *Carex wahuensis* var. *rubiginosa*° R. Krauss —variety, Hawaiian endemic

Australia
- *Carex Nealae* R. Krauss—Hawaiian endemic

Pacific North America
- *Carex macloviana* var. *subfusca* (W. Boott) Kükenth.
- *Carex pluvia* R. Krauss—Hawaiian endemic
  - *Carex pluvia* var. *koolauensis*° R. Krauss —Hawaiian endemic
  - *Carex alligata*° F. Boott—Hawaiian endemic
  - *Carex alligata* var. *Degeneri*° R. Krauss —Hawaiian endemic
  - *Carex kauaiensis*° R. Krauss—Hawaiian endemic
- *Carex Svenonis* Skottsb.

Worldwide
- *Carex montis-eeka* Hillebd.—Hawaiian endemic

°These species and varieties are presumed to have originated in the islands from the ancestral stock of the species immediately above them.

Apparently original introductions of species to the Hawaiian Islands have come from all of the major land masses bordering the Pacific. Species found in the nearest archipelagos, however, are missing in Hawaii. Others from more distant land masses are well established here. The random origin from east, west, and south, and the limited number of species present, indicate infrequent establishment over long periods of time. It is the studied opinion of the author

that winds of hurricane force sweeping across the Pacific in different directions at different periods of geologic time are responsible for this random deposition. Certainly tremendous variations in climate have existed since the origin of the islands sometime in the early Tertiary period.

Speciation and distribution of the carices of Hawaii have not followed the usual pattern found in many island genera. There are only two narrow endemics—*Carex kauaiensis* R. Krauss, which is limited to the bogs of Kauai, and *Carex pluvia* var. *koolauensis* R. Krauss, which is found in the central Koolau Range on Oahu. The other species occur on most of the islands, though certain ones are conspicuously missing on the more westerly islands. There are no records of *Carex macloviana* var. *subfusca* (W. Boott) Kükenth., *Carex Svenonis* Skottsb., or *Carex Nealae* R. Krauss on Oahu, Molokai, and Kauai. Hawaii and Maui, on the other hand, have every species and variety with the exception of *Carex kauaiensis* R. Krauss and *Carex pluvia* var. *koolauensis* R. Krauss. *Carex Meyenii* Nees, however, is the only species found on all the islands. The lack of local endemism is to be expected in a genus which fruits prolifically and is dispersed easily by air and water. Most of the species and varieties are able to survive on ridges as well as in ravines, so that geographical isolation of minor mutations does not occur often enough to be a factor in the development of taxonomic entities. Nevertheless, there appears to be some difficulty in achieving dispersal across the channels of water separating the islands. It is to be expected that a complete distribution will be achieved naturally in the future inasmuch as suitable habitats exist on all the islands for almost all of the species. The range of *Carex wahuensis* var. *rubiginosa* R. Krauss, which is moving into the region occupied by variety *Meyeri*, by migration from east to west, illustrates the path of such invasions although the habitat range for this species is considerably greater than that for some of the others.

TAXONOMIC TREATMENT

This section presents a key to and descriptions of the species of *Carex* found in the Hawaiian Islands. The key is based on characters found in the mature-fruited inflorescence. The key may be followed using perigynia alone but, wherever feasible, additional characters of inflorescence and vegetative structure are included. The key is strictly an artificial one and no implications as to natural relationship are to be drawn from it. The distribution of the species may be more readily perceived by reference to the maps. The citations of specimens examined are followed by letters designating the herbarium in which they are found. These abbreviations follow the system proposed by Lanjouw (1939: 142). If no abbreviation is included, the specimens are in the Herbarium of the Bernice P. Bishop Museum, Honolulu, T. H. The abbreviations and the institutions in whose herbaria the specimens are deposited are as follows:

C—Cornell University, Ithaca, New York
GB—The Botanical Garden, Gothenburg, Sweden
G—Conservatoire et Jardin Botanique, Geneva, Switzerland
GH—Gray Herbarium, Harvard University, Cambridge, Massachusetts
K—Kew Botanical Gardens, England
KY—University of Kyoto, Japan
NY—New York Botanical Garden, New York
P—Museum National d'Histoire Naturelle de Paris, France
US—Smithsonian Institution, Washington, D. C.
TI—University of Tokyo, Japan

The illustrations have been selected to show the range of variation within each species and variety. Three different specimens

are illustrated for each species and two for each variety.

The maps are provided with legends explaining the symbols used. Where a symbol is half-shaded the location is considered only approximate. Only those locations which could reasonably be assigned to an area as small as 1 square mile are plotted.

KEY TO HAWAIIAN *Carex*

1. Perigynium trigonal to napiform; achene with a single, invaginate furrow at the equator 2
   Perigynium trigonal to lenticular; achene with no furrow at the equator 3
2. Teeth of bidentate beak over 1 mm. in length; beak and perigynium chartaceous, green, yellow, brown, not red-waxy . . . . . **C. wahuensis** var. **Meyeri** (p. 254)
   Teeth of bidentate beak under 1 mm. in length; beak or entire perigynium red-waxy . . . . . **C. wahuensis** var. **rubiginosa** (p. 257)
3. Stigmas 3; leaves stiff, erect, strongly involute or awl-shaped 4
   Stigmas 2; leaves flexuous, not normally involute or awl-shaped . . 5
4. Mature plants over 15 cm. tall; spikes with more than 10 achenes; not dwarfed; leaves clearly involute . . . . . **C. montis-eeka** (p. 260)
   Mature plants under 15 cm. tall; spikes with fewer than 10 achenes; dwarfed; leaves awl-shaped . . **C. montis-eeka** f. **filifolia** (p. 262)
5. Perigynium multinerved, more than four nerves per side 6
   Perigynium at most three-nerved on a side or not nerved 9
6. Perigynium invaginate at the base, cordate; not stipitate . . . . . **C. Svenonis** (p. 263)
   Perigynium not invaginate at the base; stipitate 7
7. Perigynium concave-convex, spindle-shaped, winged, non-glandular; beak strongly bidentate . . . . . **C. Meyenii** (p. 264)
   Perigynium bi-convex, not winged; beak narrow, entire or subentire . 8
8. Bracts strongly emarginate; perigynium ovate, strongly nerved, minutely glandular, not purple-black; spikes gynaecandrous . . . . . **C. Nealae** (p. 267)
   Bracts acute to aristate, never emarginate, perigynium splotched with purple-black, not glandular, weakly nerved; spikes androgynous . . . **C. alligata** var. **Degeneri** (p. 278)
9. Perigynium winged, concave-convex; rostrum indistinct, tapering into the base of the perigynium; spikes short, forming a semiglobose terminal head 3 cm. in diameter or less . . . . . **C. macloviana** var. **subfusca** (p. 269)
   Perigynium not winged, bi-convex; beak distinct; spikes separate, over 3 cm. long, pendulant or erect, forming a branching inflorescence 10
10. Perigynium light brown or green, dull chartaceous to membranous . . . . . **C. pluvia** (p. 271)
    Perigynium black or brown, highly polished, indurate 11
11. Perigynium brown or yellow-brown, lenticular; one nerve on one side raised to give a trigonal aspect . . . . . **C. alligata** (p. 275)
    Perigynium black or purple-black; broad spindle-shaped, not nerved . 12
12. Perigynium not tightly packed in the spike, rachis visible, achene triangular in cross section, perigynia not stipitate . . . . . **C. kauaiensis** (p. 279)

Perigynium tightly packed in the spike, rachis not visible, achene lenticular, perigynia stipitate . . . . **C. pluvia** var. **koolauensis** (p. 274)

Carex wahuensis C. A. Meyer var. **Meyeri** Franchet and Savatier, Enum. Plant. Japon. 563, 1879.

Figs. 1*a–c*, 2

Carex wahuensis C. A. Meyer, Acad. St. Petersb., Mem. 1:218, Tab. 10, 1831.

Carex Boottiana Hooker and Arnott, Bot. Beech. Voy., 273, 1841.

Carex nupitalis Boott, Illust. Genus Carex 4, 175, pl. 591, 1867.

Rootstocks caespitose forming dense clumps to 50 cm. in diameter; basal scales 0.5–1.5 cm. wide, 1.4–4 cm. long, 4–8 per culm, soon becoming loose, fibrillose, dark brown; fertile culm 2–4 mm. wide, 15–100 cm. long, isosceles triangular in cross section, lightly scabrous or smooth on the main veins and angles, erect, heads nodding; leaves 2–15, usually 6–7, mm. wide, 5–10 cm. long, 5–8 per culm, erect for about one-third the length, scabrous and toothed on all main veins on the underside, glabrous above, shiny, dark green to yellow; sheaths loose, dark brown to reddish, closed by a dark membrane extending 4–8 cm. above the rootstock, splitting along the membrane at maturity; inflorescence 4–25 cm. long, branching, 1–4 unbranched spikes arising from a node, 2–15 nodes per culm, internodes 2–6 cm. long at the base shortening toward the apex, each node and peduncle enclosed by the base of a leafy bract; spikes 0.5–1.5 wide, 2–10 cm. long above the peduncle, androgynous except the terminal one at each node which may be entirely staminate, 1 to 3 spikes at a node enclosed by leafy bract, peduncles 2–5 cm. long, enclosed at the base by an ochrea 10–15 mm. long; pistillate bracts ovate, truncate at the base, 2–3 mm. wide, 2.5–5 mm. long, awned, hyaline on margins, red or brown membranous in the center, keeled, awns 2.5–5 mm. long, awl-shaped, toothed on margins; staminate bracts 2–5 mm. long, hyaline, keeled, awns 2–4 mm. long, toothed; perigynia 2–3.5 mm. wide, 3–8 mm. long, with

FIG. 1. Perigynia of *Carex wahuensis* C. A. Meyer var. *Meyeri* Franch. and Sav. *a, Krauss 161; b, Hitchcock 15327; c, Christophersen 3695.*

body obovoid, rarely bluntly stipitate though this condition not shown in the illustration; 20–30 nerved on a side, dull chartaceous, green to yellow or brown, rostrum 1–4 mm. long, minutely toothed on the upper third, bidentate, two teeth 0.9 mm. to 3 mm. long, spreading subulate; achene a double three-sided pyramid, distorted, invaginate at the middle or equator more strongly on one side, ridged on the angles, the planes slightly convex or concave, beak usually bent, 0.5–1 mm. long; style 1–2 mm. long, rising at right angles or less from the beak, dividing into three stigmas 2–3 mm. long.

Distribution: On all islands in Zone D of Ripperton and Hosaka (1942) in the middle forest zone in shade or on open ridges in full sun, on soil or damp rocky ravine walls.

Type: Illustrated by C. A. Meyer (1831: Table 10). The type specimen is deposited in the herbarium at Leningrad.

Specimens examined

KAUAI: *Degener 2214,* Olokele Canyon, July 3, 1926, (NY); *Degener 2207,* Hanapepe Falls, June 19, 1926, (NY); *Degener 2205,* NE of Kipu, June 17, 1926, (NY); *Fagerlind & Skottsberg 6567,* Kokee near stream opposite Phillip Rice's summer house, Mar. 12, 1948 (GB); *Heller 2849,* on Kaholuamanoa above Waimea, Oct. 1–8, 1895 (K, US); *Hitchcock 15327,* Kaholuamanu, 3500′, Oct. 20, 1916 (US); *MacDaniels 723,* Haupu, 300 m., Feb. 16, 1927; *Nuttall,* Attooi [= Kauai] (K); *St. John 10893,* Maunapuluo, Hanakapiai, Napali Coast, Dec. 30, 1930; *St. John 10817,* Nualolo Trail, 2900′, Dec. 28, 1930; *St. John 13619,* Kipu, 1100′, Dec. 25, 1933; *St. John 23087,* Olokele Ditch Trail, 2 mi. below Ditch House, Dec. 26, 1947; *St. John 23142,* rocky base of cliff, Waiahuakua Valley, 1500′, Dec. 29, 1947; *St. John 22880,* Waimea Trail, Kokee, 3700′, Dec. 21, 1947; *St. John 23194,* West branch of Hanakoa Valley, 1000′, Dec. 31, 1947; *St. John 23078,* Olokele Ditch Trail, 1427′, Dec. 26, 1947; *St. John & Fosberg 13717,* Milolii Ridge, 1600′, Dec. 27, 1933; *St. John & Fosberg 13718,* Milolii Ridge, 2000′, Dec. 27, 1933; *Skottsberg 1043,* Olo-

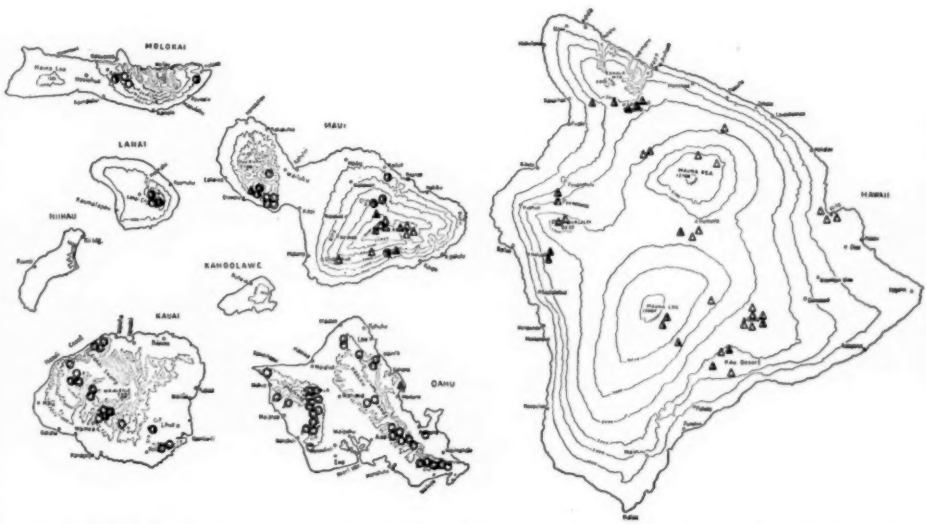

FIG. 2. Distribution of *Carex wahuensis* C. A. Meyer var. *Meyeri* Franch. and Sav. (indicated by circles) and of *C. wahuensis* C. A. Meyer var. *rubiginosa* R. Krauss (indicated by triangles).

kele Canyon, Oct. 21, 1922; *Smith, Whiting, Neal,* Kokee, 3500′, May 1, 1929.

OAHU: *Bryan 706,* Mt. Kaala, 900 m., Apr. 21, 1929; *Christophersen 3677,* below Kanehoa, 400 m., June 1, 1932; *Christophersen 3695,* below Kanehoa, 350 m., June 1, 1932; *Christophersen, Wilder, Hume 1526,* Kuliouou, 450–600 m., Feb. 5, 1931; *Christophersen, Wilder, Hume 1549,* below Puu Kapu, 350–500 m., Feb. 12, 1931; *Cowan 851,* ¼ mi. N of Puu Kaua, Feb. 29, 1948; *Cowan 955,* Halawa Ridge Trail, Apr. 25, 1948; *Cowan 814,* ridge trail to Palikea, Feb. 4, 1948; *Degener 8272,* head of Kuliouou Valley, Dec. 11, 1927, (NY); *Degener 8218,* small valley E of Palikea, Oct. 23, 1932, (NY); *Degener 5268,* Kolekole Pass, May 1, 1926, (NY); *Degener 8220,* top of Kaena Pt., Jan. 31, 1932, (NY); *Degener 8221,* Pupukea, Kahuku Trail, Pupukea side, Mar. 30, 1927, (NY); *Degener 8281,* near summit of Kaala, Feb. 11, 1928, (NY); *Degener 5263,* E ridge of Manoa Valley, Feb. 6, 1927, (NY); *Degener 8219,* first gully S side of Keaau Valley, Feb. 7, 1932, (NY); *Degener 19581,* Mokuleia mauka, 2000′, May 2, 1949; *Fagerlind 6459,* trail to Puu Kaua, Feb. 29, 1948, (GB); *Forbes 1471.0,* Lanihuli Trail, Mar. 15, 1910; *Forbes 2518.0,* Waialae Valley, Jan. 8, 1919; *Forbes 2425.0,* Waialae iki, Feb. 28, 1917; *Forbes 2466.0,* ridge between Niu and Wailupe, Apr. 11, 1917; *Forbes 2523.0,* Wailupe, Jan. 1919; *Fosberg 13552,* Kailua, Ulumawao, 130 m., Jan. 24, 1937; *Fosberg 12281,* Nuuanu Pali, 370 m., Oct. 14, 1935; *Fosberg 9273,* Palolo Valley, 425 m., Mar. 19, 1933; *Fosberg 13799,* Nanakuli Valley Head, 825 m., May 2, 1937; *Fosberg 13007,* Puu Kalena, 930 m., Mar. 22, 1936; *Heller 2389,* lower slopes of Waiolani, June 6, 1895; *Hillebrand 560,* Nuuanu Valley, 1860–67; *Hitchcock 13788,* Nuuanu Pali, June 17, 1916; *Hitchcock 14049,* Nuuanu Pali, July 19, 1916; *Hosaka 540,* Kipapa, 1000′, May 15, 1932; *Hosaka 948,* Kipapa Gulch 1800′, Mar. 19, 1933; *Hume 482,* Puu Kanehoa, 1500′, Jan. 18, 1932; *Krauss 183,* SE slope of Kaala, 3000′, Apr. 18, 1948; *Krauss 247,* trail along Wiliwilinui ridge, 1450′, June 28, 1948; *Krauss 243,* trail along Wiliwilinui ridge, 1300′, June 28, 1948; *Krauss 126,* trail to Puu Kaua, 2800′, Feb. 29, 1948; *Krauss 123,* trail to Puu Kaua, 3000′, Feb. 29, 1948; *Krauss 121,* trail to Puu Kaua, 3000′, Feb. 29, 1948; *Krauss 140,* ridge S of Maakua Gulch, 800′, Mar. 21, 1948; *Krauss 161,* Palikea, 2800′, Mar. 26, 1948; *Krauss 114,* Palikea, Feb. 4, 1948; *Krauss 109,* Palikea, Feb. 4, 1948; *Krauss 108,* Palikea, Feb. 4, 1948; *Krauss 188,* Kaala, 3000′, Apr. 18, 1948; *Krauss 196,* Kaala, 2000′, Apr. 18, 1948; *Krauss 197,* Kaala, 2000′, Apr. 18, 1948; *Krauss 198,* Kaala, 3000′, Apr. 18, 1948; *Krauss 199,* Kaala, 2500′, Apr. 18, 1948; *Krauss 111,* Palikea, 3000′, Feb. 4, 1948; *Krauss 140,* ridge of Maakua, 600′, Mar. 21, 1948; *Krauss 561,* N fork of Elehaha Stream, 865′, Apr. 16, 1949; *Nuttall,* Oahu, (K); *Remy 142,* Oahu, 1851–55, (GH, P); *St. John 10440,* Puu Hapapa, Waianae Mts., 2800′, Mar. 16, 1930; *St. John 21569,* Waimanalo, 750′, Mar. 24, 1946; *St. John 10385,* Palikea, 1200′, Feb. 23, 1930; *St. John 17612,* Puu Kawiwi, 2800′, Mar. 31, 1935; *St. John 20182,* Kaluanui Ridge, 1500′, Feb. 16, 1941; *St. John 13154,* Pohakea Pass, 2100′, May 12, 1933; *St. John 10441,* Puu Hapapa, 1700′, Mar. 16, 1930; *St. John 14059,* E of Puu Kanehoa, 2350′, Jan. 7, 1934; *St. John 13047,* Laie-Malaekahana ridge, 1100′, Apr. 15, 1933; *St. John 11044,* Puu Kanehoa, 2700′, Mar. 22, 1931; *St. John 14018,* Puu Kanehoa, 2700′, Jan. 7, 1934; *St. John 13037,* Kalauao ridge, 1500′, Mar. 29, 1933; *St. John 11069,* Puu Kanehoa, 2000′, Apr. 22, 1931.

MOLOKAI: *Degener 8239,* ravine NW of Mauna hui, May 27, 1928; *Degener 8238,* Kahuaawi Gulch, May 12, 1928; *Degener, 8230,* ravine, S of Mauna hui cabin, Apr. 15,

1928; *Fagerlind & Skottsberg 6376,* along road from Mapulehu to Halawa, E coast, Feb. 20, 1948, (G).

LANAI: *Fagerlind & Skottsberg 6418,* W side of main ridge near Munro's old place, Feb. 24, 1948, (G); *Hitchcock 14690,* ravine at foot of mountain, Sept. 21, 1916, (US); *Munro 408,* Pohaku, Feb. 27, 1915, (US); *Munro 297,* Kaiholena, Feb. 17, 1914; *St. John & Cowan 22609,* SW ridge of Kaiholena Gulch, Kamoku, 2300′, Apr. 4, 1947; *St. John & Cowan 22612,* SW ridge of Kaiholena Gulch, Kamoku, 2200′, Apr. 4, 1947.

MAUI: *Degener 8244,* Manawainui Gulch near Puu Anu, dry side, July 12, 1927, (NY); *Degener 8243,* Manawainui Gulch near Puu Anu, dry side, July 12, 1927, (NY); *Degener 8246,* ridge N of Popakea Gulch, July 23, 1927, (NY); *Degener 8254,* hill mauka of Olinda, June 15, 1927, (NY); *Degener 8247,* ridge N of Popakea Gulch, July 23, 1927, (NY); *Degener 8249,* along pipe-line trail, Olinda, June 22, 1927, (NY); *Forbes 2338.M,* Olowalu Valley, May 2, 1920; *Forbes 2285.M,* Olowalu Valley, May 9, 1920; *Forbes 2339.M,* Olowalu Valley, May 12, 1920; *Forbes 1862.M,* Waiopaa Ranch, Nuu, Mar. 6, 1920; *Remy 143,* Maui, 1851–55, (P); *Rock 8747M,* Makaima, Apr. 1911; *Rock 8753M,* shore at Nahiku, May 10, 1911; *St. John 10280,* Iao Valley, 1200′, Feb. 9, 1930.

HAWAII: *Spach,* Owhyhee, Jan. 1859, *(K).*

SANDWICH ISLANDS: *Hillebrand* (Erroneously as Hillebrant) *2328,* Sandwich Islands, 1860–67, (US), (immature).

Carex wahuensis C. A. Meyer is a member of the subgenus *Eucarex* Coss. & Germ. (Kükenthal, 1909: 293) section *Rhomboidales* Kükenth. (Kükenthal, 1909: 622). It is easily distinguished from the other Hawaiian species by the deep groove in the achene. Its apparent origin is in the western Pacific, the Hawaiian members being only slightly different from those of Japan. Names placed in synonomy were created by authors who felt they could segregate new species or by those who received specimens from areas distant from Oahu and expected no similarity. These are *Carex Boottiana* Hooker and Arnott (Hooker, 1841: 273) collected from Japan, and *Carex nupitalis* Boott (Boott, 1855: 175) from Hawaii. Boott was misled by the distorted appearance of the immature fruit so clearly shown in his Plate 591. This plate is based on *Remy 142* from Oahu and on a single spike from Nuttall's collection. Variety *Meyeri* of Franchet and Savatier was made after an examination of the species collected in the Hawaiian Islands and those from Japan and the Bonins. The variety *Meyeri* was apparently created from the material of Remy in order to have a contrasting variety to variety *robusta* from Japan and variety *Bongardii* from the Bonins. The only citation of the habitat of variety *Meyeri* is "ex speciminibus herbarii Mus. Parisiensis." Earlier in their discussion of the contrasting characters of the two varieties *robusta* and *Bongardii* as opposed to those in the species, they mention that they are compared to the plants collected by Remy in the Paris Herbarium. It is apparent that the intent of Franchet and Savatier was to make a variety corresponding to variety *typica* as now used. The International Rules, in Recommendation 18, specify that new names should not be used for the variety containing the type of the species but instead such names as *typicus, genuinus,* etc. The use of another name for the typical variety is not definitely prohibited, however. Therefore the variety *Meyeri* must be accepted as the variety of *Carex wahuensis* C. A. Meyer containing the original species.

The type specimen was not seen but C. B. Clarke (1904: 319) in his discussion of *Carex Wilfordii* C. B. Clarke says that the type corresponds well with Tab. 10 of Meyer.

Carex wahuensis C. A. Meyer var. **rubiginosa** var. nov.

Figs. 2, 3*a–d*

A specie differt in utriculis 2.5–4 mm. latis,

3–8 mm. longis trigonis obovoideis aut obnapiformis valde multinervosis ad debilitibus nervosis, in rostris et prope omnis corporis utriculis rubri-cereis, rostris 1.5–3 mm. longis bidentatis angustis, dentibus 0.15–0.9 mm. longis, — 0.9 mm. longis solum in exemplis grandissimis.

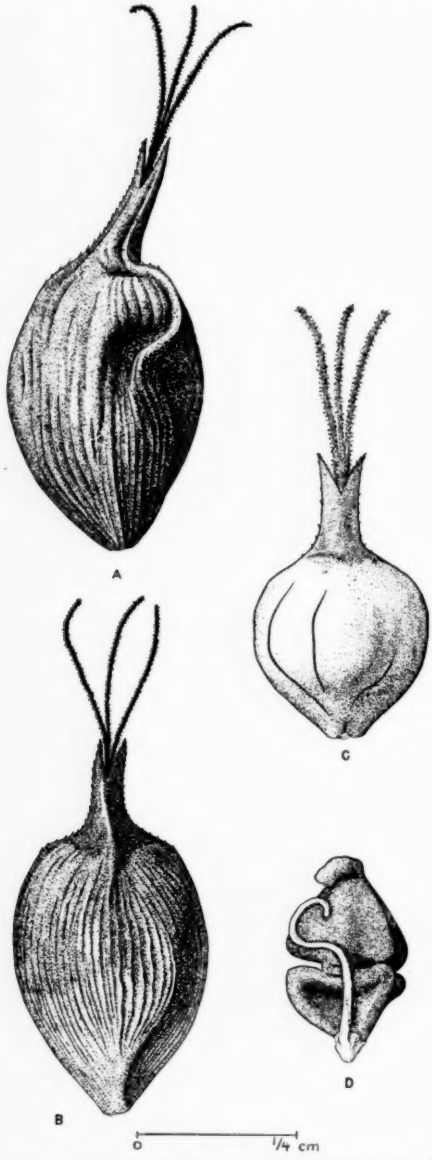

FIG. 3. *Carex wahuensis* C. A. Meyer var. *rubiginosa* R. Krauss. *a–c*, perigynia; *d*, achene. *a*, *Degener 2218; b, Forbes 172.H; c, d, Krauss 348.*

Similar to the species except in following characters: Perigynia 2.5–4 mm. wide, 3–8 mm. long, broad-obovoid to obnapiform tapering to a truncate base, roughly 3-angled strongly multi-nerved or obscurely several-nerved, bright red-waxy on rostrum and usually on most of the surface of the perigynium, rostrum bidentate, 1.5–3 mm. long, narrow, teeth 0.15–0.9 mm. long, approaching 0.9 only in very large individuals.

Distribution: On Hawaii, Maui, rarely Oahu, in Zones D and E of Ripperton and Hosaka (1942), in the upper forest in dry sunny cliff faces and open meadows, seldom in shade, usually over 4,000 feet.

Type: H. St. John, R. S. Bean, and E. Y. Hosaka 11228, Kilauea Iki, 3930′ alt., Dec. 21, 1931.

Specimens examined

OAHU: *St. John 11080,* Kaaawa Valley, 800′, Apr. 12, 1931.

MAUI: *Degener 5262,* Haleakala, (NY); *Degener 8241,* N of Ulupalakua, July 4, 1927, (NY); *Degener 8250,* Haleakala near Koolau Gap, June 29, 1927, (NY); *Degener 8265,* Koolau Gap, Haleakala Crater, Aug. 11, 1927, (NY); *Degener 8270,* Haleakala Crater, Aug. 9, 1927, (NY); *Forbes 296.M,* Haleakala, Aug. 1910; *Forbes 698.M,* NE of Ukulele, July 9, 1919; *Forbes 1089.M,* Haleakala Crater, Aug. 8, 1919; *Forbes 2285.M,* Olowalu Valley, May 9, 1920; *Forbes 1876.M,* Waiopaa Ranch, Mar. 6, 1920; *Forbes 1887.M,* Puu Pani, Mar. 8, 1920; *Forbes 2104.M,* Auwahi, S slope of Haleakala, Mar. 24, 1920; *Forbes 2141.M,* Puu Ouli, Haleakala, 4300′, Apr. 4, 1920; *Forbes 2143.M,* Puu Ouli, Haleakala, 4300′, Apr. 4, 1920; *Fosberg 9928,* Haleakala between bottomless pit and pali, 2150 m., Sept. 23, 1933; *Hillebrand,* Haleakala, (K); *Hil-*

lebrand 531, Haleakala, 7000′, (K); *Krauss 346,* cliffs above Holua, 7000′, Sept. 3, 1948; *Krauss 348,* cliffs above Holua, 7000′, Sept. 3, 1948; *Krauss 349,* cliffs above Holua, 7000′, Sept. 3, 1948; *Krauss 352,* cliffs above Holua, 7000′, Sept. 3, 1948; *Remy 144,* 1851–55, (P); *Rock 8750,* Haleakala, 8000′, Apr. 20, 1911.

HAWAII: *Degener 2218,* E of Kilauea-iki, July 17, 1926, (NY); *Degener 2217,* 17 mi. from Kohala to Waimea, July 31, 1932, (NY); *Degener 2215,* between N Kona and Kau Desert, July 15, 1926, (NY); *Degener 2219,* W of Kilauea along Kau Rd., July 21, 1926, (NY); *Degener H103,* Haw. Nat'l Park, moist forest near Kilauea-Iki, Dec. 21, 1922, (NY); *Degener 19262,* Nenenui, central plateau, Sept. 17, 1948, (NY); *Ewart 326,* Hanaipae, 5000′, Feb. 14, 1934; *Fagerlind & Skottsberg 6242,* truck road between Kilauea and Mauna Loa, 6000′, Feb. 2, 1948, (GB); *Faurie 1214,* shore of Hilo, May 1909, (G); *Forbes 172.H,* Hanehane, Kona, June 15, 1911; *Forbes 914.H,* Flow of 1880, Kipuka-ahui, June 23, 1915; *Forbes 9039.H,* Mauna Kea above Lai Niaia, June 18, 1915; *Fosberg 10114,* between Makaopuhi and Napau Craters, Kilauea, 890 m., Aug. 29, 1933; *Hillebrand 1960,* Hilo, (US); *Hillebrand 532,* Hilo, (K); *Hinds 2,* 1841, (K); *Hitchcock 14433,* Humuula Sheep Station, 6000′, Aug. 27, 1916, (US); *Hitchcock 14477,* Puu Waawaa, Aug. 30, 1916, (US); *Hitchcock 15592,* Hualalai Mt. summit, Aug. 25, 1916, (US); *Hitchcock 14224,* Kukaiau Ranch, 3600′, Aug. 20, 1916, (US); *Hitchcock 14283,* Mauna Kea, N side, 800–1000, Aug. 22, 1916, (US); *Judd,* Waikii, July 21, 1928; *Macrae,* Kaaha, June 1825, (K); *Mann & Brigham 328,* summit of Hualalai, 1867, (G); *Meebold,* Kipuka Puaulu, Kilauea, May 1932; *Neal & Hartt 666,* Base of Puu Hulukulu, 6610′, Aug. 6, 1935; *Nuttall 3,* (K); *Remy 145,* 1851–55, (P); *Rock 8741,* Kilauea Volcano, Apr. 1911; *Rock 8411,* Waikii, June 1910; *Rock 8742,* Kilauea Volcano, Apr. 1911; *Rock 10042,* Pulehua, Jan. 1912; *St. John 11333,* Manuka Mauka, 1700′, Dec. 26, 1931; *St. John, Bean, and Hosaka 11228,* (See Type); *St. John & Cowan 22312,* Halfway House, Kau Desert, 2900′, Dec. 23, 1946; *St. John 11220,* chain of craters, Napau Trail, 2750′, Dec. 30, 1931; *Skottsberg 1103,* between Kilauea and Kapapala, Sept. 18, 1922, (GB); *Skottsberg 633,* S slope of Hualalai, 1200 m., Sept. 23, 1922, (GB); *Skottsberg 633b,* Hualalai, 2000 m., Sept. 24, 1922, (GB); *Skottsberg 1874,* Kilauea Iki, Sept. 21, 1926; *Skottsberg 517,* E slope of Mauna Loa, Sept. 15, 1922; *Wilkes Exped.,* crater W Lua Pele, 1838–42, (US); *Wilkes Exped.,* district of Waimea, 1838–42, (US); *Wilkes Exped.,* Mauna Loa, 1838–42, (US); *Wilkes Exped.,* Mauna Loa, above 8000′ station, 1838–42, (US).

SANDWICH ISLANDS: *Hillebrand 2325,* Sandwich Islands 1860–67, (US); *Hillebrand 2327,* Sandwich Islands 1860–67, (US).

Carex wahuensis Meyer var. *rubiginosa* is the only possible segregate in this species. A detailed tabulation, with careful measurements and repeated observations, was made of each specimen examined. It soon became apparent that the population was one of many different biotypes varying in stature as well as in floral structure. Every possible character was used to separate the plants into logical natural groups. Only two characters seemed usable and they were occasionally difficult to distinguish even to the trained eye. One is the red-waxy color of the perigynia of plants from Hawaii and Maui. The other is the very short teeth, usually only 0.5 mm. in length, of the beak of the perigynia. Other characters believed infallible in *Carex*—such as structure and shape of the perigynia, setaceousness of the rostra, and complexity of inflorescence—proved unreliable. A surprising number of apparently teratological forms occurred in various collections as follows:

Hosaka 540, Kipapa Gulch, Waipio, S ridge, 1000′, May 1932: a complete androgynous spike arising from a perfectly formed utricle

Krauss 348: an extension of the axis within the perigynia reminiscent of the barb in *Uncinia*

Rock 8753, at the shore, Nahiku, Maui, May 10, 1911: a compounding of the spikes by numerous branchings from the base of each normal one to form a dense head

Forbes 1862.M: extremely large fruit as much as three times as large as normal

Carex montis-eeka Hillebrand, Flora of the Hawaiian Islands 486, 1888.

Figs. 4*a–c*, 5

Carex montis-eeka Hillebd. var. *viridens* Kükenth., Fedde Rep. 16: 435, 1920.

Rootstocks loosely caespitose; basal scales 7–8 mm. wide, 10 cm. long, 2–5 per culm, reddish, persistent; fertile culm, 2–3 mm. wide, 75 cm. long, with cross section triagonal to semicircular, smooth, strongly veined, hollow, distinct from the leaves near the base, stiffly erect; leaves 1–2 mm. wide, 70 cm. long, 5–8 per culm, stiffly erect, clumped, strongly involute, glabrous, dark green; sheaths 15 cm. long, closed by a tight hyaline membrane; inflorescence 5–10 mm. wide, 2–7 cm. long, with 2–5 nodes, one spike to a node, lower internodes 1–3 cm. long, upper internodes shortened to 1–2 mm., or all spikes arising from a common terminal node; spikes androgynous except terminal spike which is staminate, 3–5 mm. wide, 1–3 cm. long, sessile or short pedunculate with an open ochrea at the base adjacent to the culm; pistillate bracts 1.5 mm. wide, 3 mm. long, ovate, chartaceous, 1–3-nerved, glabrous, green to brown; staminate bracts 4–5 mm. long, lanceolate, acuminate, 1–3-nerved; perigynia ovoid to lanceoloid, concave-convex to bi-convex, 1.5–2 mm. wide, 3–5 mm. long, toothed on the upper third of the margin, otherwise smooth, 1–3 nerved near the center on the convex side, singly nerved or not nerved on the concave side, rostrum tapering to a shallowly bidentate apex; achenes isosceles triangular in cross section, obovate, 2–2.5 mm. wide, 1.5 mm. long, truncate at the base, rugose, smooth and slightly ridged at the angles, light brown, rostrum 0.2 mm. long, bent back on the achene; style 1 mm. long dividing into three stigmas 2–3 mm. long, dark brown, glandular.

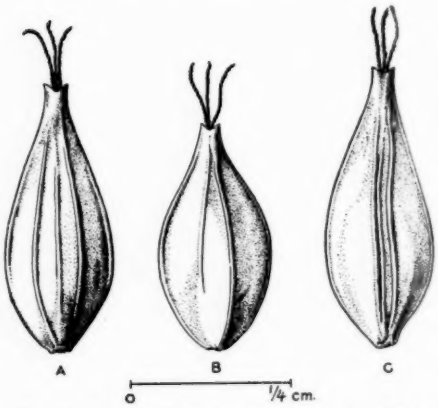

FIG. 4. Perigynia of *Carex montis-eeka* Hillebd. *a. Forbes 418.K, b, Fosberg 10039; c, Degener 8264.*

Distribution: on Kauai, Molokai, and Maui, in Zones D_3 and E_1 (Ripperton and Hosaka, 1942), the middle forest bog zone, in extremely wet, high bogs above 3,800 feet or in ponds in the bogs.

Lectotype: J. F. Rock 8190, summit of Puu Kukui, West Maui, Aug. 21, 1910.

No types or isotypes collected by William Hillebrand are available. The specimens were in the Berlin Herbarium, which was destroyed by fire in 1944. The entire collection of the Cyperaceae was lost. The collection of Rock cited above as the lectotype is from the same area as that cited by Hillebrand and contains many duplicates. It has been established that

the Hillebrand specimens cited as being from Mt. Eke are actually from Puu Kukui, the only area in which he collected in this high bog region.

Specimens examined

KAUAI: *Cranwell, Selling, and Skottsberg 2870,* Alakai between Lehua makanoe and Kilohana, Aug. 15, 1938; *Degener 2204,* Waineke, June 28, 1926, (NY); *Faurie 1204,* Hanapepe, Dec. 1909, (KY); *Forbes 418.K,* Kaholuamanu behind Waimea, Sept., 1908; *Forbes 881.K,* Alakai Swamp, Waimea drainage basin, west side, July 3–Aug. 18, 1917; *Forbes 1155.K,* Alakai Swamp, Waimea drainage basin, July 3–Aug. 18, 1917; *Hitchcock 15488,* Waialeale, 3600–5080′, Oct. 22–24, 1916, (K); *Hitchcock 15515,* Kauluwehi Swamp, near Kaholuamanu Bog, Oct. 25, 1916, (K); *Rock 9016,* Kauluwehi Swamp, Waimea drainage basin, July 3–Aug. 18, 1917; *St. John 10773,* NW end of Alakai Swamp, Na Pali, 3800′, Dec. 27, 1931; *St. John 13569,* Kahili Bog, 2100′, Dec. 24, 1933; *Skottsberg 943,* Alakai Swamp near Kilohana, 1500 m., Oct. 27, 1922.

MOLOKAI: *Cranwell, Selling, Skottsberg 2529,* Pepeopae Bog, July 7, 1938; *Degener 8235,* Pepeopae Bog, May 3, 1928, (NY); *Degener 8237,* Pepeopae Bog, May 8, 1928, (NY); *Forbes 199.Mo,* mountains above Puu Kolekole, July 1912; *Hitchcock 15192,* central Molokai bog, 4000′, Oct. 13, 1916; *Munro 379,* above Pelekunu, May 6, 1916; *Munro,* Kaunakakai, Jan. 1904; *St. John 12560,* Kawela ridge between Hanalilolilo and Pepeopae, 4100′, Dec. 25, 1932.

MAUI: *Bryan 641,* Puu Kukui, 5200′, Dec. 20, 1928; *Degener 8258,* Mt. Ekee, Aug. 29, 1927, (NY); *Degener 8257,* Mt. Ekee, Aug. 30, 1927, (NY); *Degener 8264,* Mt. Ekee, Aug. 27, 1927, (NY); *Ewart 78,* Puu Kukui, pond, 4800′, Dec. 18, 1928; *Ewart 45,* Puu Kukui, 5700′, Dec. 20, 1928; *Forbes 465.M,* Eeke-Honokahau drainage basin, Sept. 25–Oct. 1917; *Forbes 1182.M,*

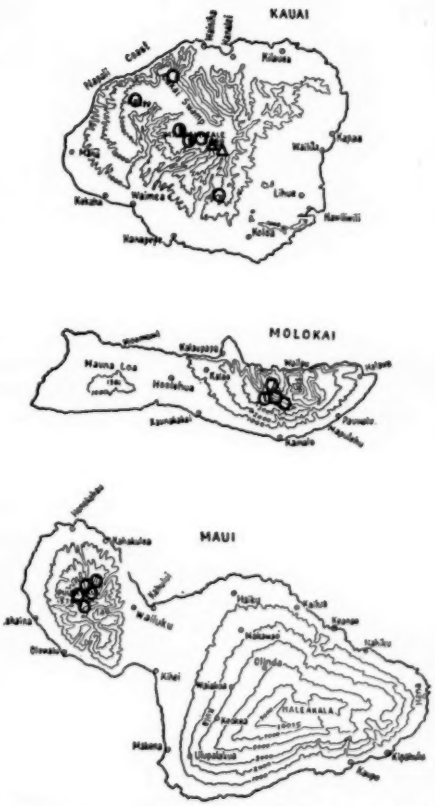

FIG. 5. Distribution of *Carex montis-eeka* Hillebd. (indicated by circles) and of *C. montis-eeka* forma *filifolia* (Skottsb.) R. Krauss (indicated by triangles).

Waianapanapa Haleakala, Aug. 20, 1919; *Fosberg 10039,* Puu Kukui, pool, 1700 m., Aug. 24, 1933; *Hitchcock 14840,* Puu Kukui, 5000′, Sept. 24–26, 1916; *Krauss 424,* Puu Kukui, 5500′, Sept. 8, 1948; *Krauss 468,* Puu Kukui, 5300′, Sept. 10, 1948; *Rock 8190,* Summit of Puu Kukui, Aug. 21, 1910; *St. John 10262,* Puu Kukui, 5750′, Feb. 7, 1930; *Skottsberg 741,* top bog of Kukui, 1800 m., Sept. 10, 1922.

Carex montis-eeka Hillebd. is the only Hawaiian representative of section *Extensae* Fries (or *Spinostachyeae* of Drejer) (Küken-

thal, 1909: 657). The section is widespread, occurring on all the continents, with a particular complex in Australia. As judged from written descriptions and plates *Carex montis-eeka* Hillebd. seems to approach *Carex serotina* Merat. (*Carex Oederi* Retz.) (Kükenthal, 1909: 301–303). It differs in the central nature of the perigynial veining, and in the extreme rigidity of the culm and involute leaves found in *Carex montis-eeka* Hillebd.

Skottsberg (1944: 333) uses the spelling *montis-Eke*, applying Article 70 of the International Rules of Nomenclature. The capitalization of Eke is permissible (Art. 70, note 1), but there is no indication that "eeka" is an unintentional typographic or orthographic error even if it may be a corruption of the present spelling for Mount Eke. The original spelling must be retained in the absence of such proof.

Kükenthal (1909: 435) describes *Carex montis-eeka* var. *viridens* as follows: "Squamae tenuiores pallidiones. Utriculi squamos large superantes oblique patentes virides nitidi oblongo elipsoidei, in rostrum magis conspicuum emarginatum abeuntes. Sandwich Inseln: Kauai, Hanapepe (Faurie no. 1204)." The type was secured and examined for these characters. The bracts are scarcely shorter than the large perigynia. They are slightly more hyaline than is usual but certainly not exceptional enough to indicate genetic difference. The rostra are only slightly more strongly bidentate than those in the rest of the population. Other Kauai specimens were examined to determine the constancy of the characters given. *Cranwell, Selling, and Skottsberg 2807*, collected in the region of the Faurie number, has the characters given by Kükenthal. The perigynia exceed the bracts by at least half their length; they are at an oblique angle with the rachis; they are green and shiny; and there is a slight groove in the rostrum. From the fresh stigmas it is clear that this is an immature specimen. The scales are still green and in growing condition, the lower older ones already much larger than the upper ones. The characters given are all those of a young inflorescence. None of the other Kauai specimens shows these features except in the more immature spikes.

Carex montis-eeka Hillebrand f. **filifolia** (Skottsberg) comb. nov.

Fig. 5

Carex montis-Eke var. *filifolia* Skottsb., Acta Horti. Gotob. 15: 333, 1944.

Fruiting plants like those of the species but dwarfed; fertile culms 10–12 cm. tall, rarely to 33 cm. tall; leaves 0.1–0.5 mm. wide, 10–15, rarely 25, cm. tall, awl-shaped, channeled; inflorescence of 2–3 spikes, 3–6 perigynia per spike.

Type: L. M. Cranwell, O. Selling, C. Skottsberg 3042, summit of Waialeale, Kauai, Aug. 23, 1938.

Species examined

KAUAI: *Cranwell, Selling, Skottsberg 3059*, summit region of Waialeale, Aug. 23, 1938; *Cranwell, Selling, Skottsberg 3042*, (See Type); *Rock 12754*, Waialeale Swamp, Oct. 10, 1911.

Carex montis-eeka Hillebrand var. *filifolia* Skottsberg is retained as a form although only three specimens have been collected and one of these is less distinct than the others. Essentially, the difference is in the dwarf filiform aspect of the vegetative parts. Inspection of the plants, however, indicates that the rhizome is an old one and the growth habit is constant. The plant is found only on Mount Waialeale in Kauai well within the geographic and ecologic range of the species.

The variety is being reduced to a form not out of a desire arbitrarily to change categories but from the belief that this form is an unusual biotype of the species only ecologically modified to the stature at hand. Further collections of a large mass of material

of this form might indicate that it is a true variety with hereditary characters. On the other hand further collections of intermediates would validate the view now taken or cause complete union of this population with that of the species.

Carex Svenonis Skottsberg, Acta Horti. Gotob. 15:329–333, 1944.

Figs. 6*a–c*, 7

Carex Svenonis var. *alakaiensis* Skottsb., Acta Horti. Gotob. 15:330–333, 1944.

Rootstocks caespitose, freely branching; basal scales 2–3 mm. wide, 0.5–2.5 mm. long, 1–3 per culm, fibrillose, caducous, brown, many fertile culms in a tuft (10–15 per 16 sq. cm.); fertile culm unequally triagonal, slender, broadest side 0.5–0.9 mm. wide, 25–30 cm. long, faces slightly concave, glabrous, pendent to erect; leaves filiform to slender, pendent at the ends, three-sided, deeply grooved on one side near the base, slightly so at the tip, scabrous on the three sides, light green; sheaths broad, membranous, enclosing culm and younger leaves up to 8 cm. above the rootstock, tight, brown to green; inflorescence 5 mm. wide, 2–5 cm. long, 3–7 spikes per culm, one spike per node, the lower nodes 1 cm. apart, the upper closer, each spike subtended by a leafy bract which narrows at once to a filiform, scabrous awn, 0.5–8 cm. long; terminal spikes staminate, lateral spikes androgynous, gynaecandrous, or both, 3–4 mm. wide, 3–12 mm. long, sessile, subtended within the leafy bract by a large bract or scale; pistillate bracts 1.5 mm. wide, 1.5–2.8 mm. long, broad ovate to triangular, hyaline with a single broad, dorsal nerve, acuminate, smooth on margins; staminate bracts similar, slightly reduced; perigynia 1–1.5 mm. wide, 1.5–3.5 mm. long, ovoid, convex-concave, strongly invaginate or cordate at the base, sessile or short stipitate, distinctly 5–9-nerved, glabrous, rostrum indistinct, scarcely separate from the gradually tapering body, broad, toothed, the apex unequally shallowly bidentate, frequently splitting down the entire length of the perigynia along a weakened line in the center of the convex side; achenes ovate, stipitate, glabrous, tan; style 0.5 mm. long, dividing into two stigmas 2–3 mm. long, tapering, glandular, reddish.

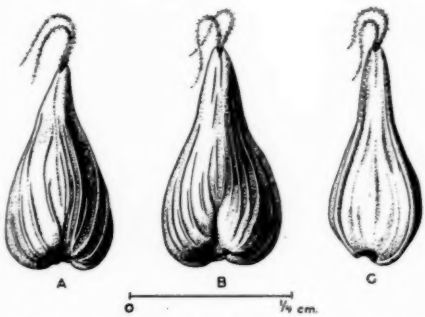

FIG. 6. Perigynia of *Carex Svenonis* Skottsb. *a, Forbes 934.H; b, Forbes 1181.M; c, Forbes 934.H* (ventral side).

Distribution: Hawaii and Maui above 5,000 feet in Zones D_3 and E of Ripperton and Hosaka (1942), in bogs or wet regions of the upper forest.

Type: S. Berggren, Aug. 1875, Hawaii, in silva montis Mauna Kea.

Specimens examined

MAUI: *Forbes 1181.M,* Bog below Waianapanapa, Aug. 20, 1919.

HAWAII: *Degener 19223,* 29 miles, Kilauea, June 7, 1929, (NY); *Forbes 934.H,* In 1880–1 flow below Kipuka ahiu, June 24, 1915; *Skottsberg 6781,* Piihonua, on Puu Oo trail near crossroad, Apr. 7, 1948.

This species is a member of subgenus *Vignea* Beauv. (Kükenthal 1909:111), section *Elongatae* Kunth (Kükenthal 1909:226). This section presents a large number of species of worldwide distribution. The characters differentiating the species are so minor that the vast majority must be reduced to synonymy. Mackenzie lists a group of 19 species under section *Stellulatae* of Kunth.

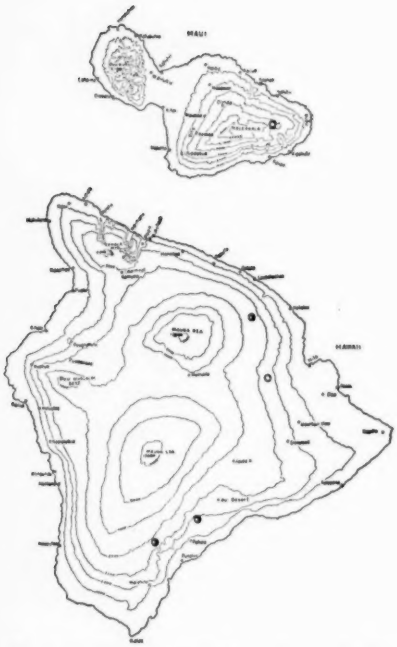

FIG. 7. Distribution of *Carex Svenonis* Skottsb.

The characters used to differentiate these species—the shape of the teeth on the margins of the perigynia; intensity of nerving, width of leaf blades, etc.—are not reliable. Kükenthal has split the species *Carex stellulata* Good into 12 varieties and forms on characters little better than these but which conform to likely geographical distribution. It is felt that his more conservative treatment is more nearly the one to be accepted.

In his discussion of the new species *Svenonis,* Skottsberg (1944:330) writes at length concerning its status. He points out clearly the difficulties involved in placing the new plant in the midst of a confusion of closely related species which have not been critically monographed. His conclusion is, "It is possible that *Carex Svenonis* does not deserve the rank of a species, certainly not if *Carex echinata (stellulata)* is taken in the wider sense of Kükenthal. In any case it is an addition to the Hawaiian flora." Skottsberg does not give enough evidence to delineate a new species from others in section *Stellulatae.* The only character that is of value is the occurrence on some culms of staminate terminal spikes, but this character is found in certain of the North American species (*Carex bromoides* Schkuhr.) and, according to Kükenthal, it also occurs in the species *stellulata* as well as in the section *Elongatae.* However, the species that are published must be critically revised for the world. No helpful decision can be reached for one species without a study of the entire sections *Stellulatae* Mack. and *Elongatae* Kunth. It seems unwise at this time to state that *Carex Svenonis* cannot be distinguished from any of many closely related species, when it is not even possible to determine those species from which it cannot be distinguished. *Carex Svenonis* and a large number of untenable segregates must be retained until that revision is made.

Carex Meyenii Nees, Nova Acta Acad. Leop., Carol. Nat. Cur. 19, Suppl. I, 1843.

Figs. 8*a–c*, 9

Carex Remyi Boeckeler, Flora 58: 269, 1875.

Carex brunnea Thunb. var. β Hillebd., Flora of the Hawaiian Islands 489, 1888.

Carex brunnea var. *Meyenii* Kükenth. Engler's Pflanzenreich IV, 20:601, 1901.

Rootstocks caespitose forming clumps to 40 cm. in diameter; basal scales 3–5 mm. wide, 0.5–1.5 mm. long, 5–10 per culm, ovate, multinerved, rich brown; fertile culm, 1–1.5 mm. wide, 30–60 cm. long, sharply triagonal, smooth below, lightly scabrous above, pendent to semi-erect; leaves 2–3 mm. wide, 30–60 cm. long, 5–15 per culm, dark green; pendent narrow, lightly scabrous on main veins and margins, sheaths tight, closed by a hyaline, deeply notched membrane ex-

FIG. 8. Perigynia of *Carex Meyenii* Nees. *a, St. John & Catto 17613; b, St. John 10382; c, Rock 8752.*

tending 5–10 cm. above the rootstock, dark brown at the base; inflorescence 5–25 cm. long, pendent, 4–6 spikes arising from a node, 4–10 nodes per culm, each node subtended by a leafy bract 8–15 cm. long, lower internodes 2–4 cm. apart, upper internodes shortened, upper leafy bracts reduced to scales; spikes 2–3 mm. wide, 2–4 cm. long, androgynous, peduncles 1.5–3 cm. long, with membranous tubular cladoprophylla or ochreas 2–3 cm. long; pistillate bracts 1 mm. wide, 3 mm. long, hyaline, keeled, obscurely nerved; staminate bracts 0.8 mm. wide, 4 mm. long, lanceolate, keeled, hyaline-margined; perigynia 1–1.5 mm. wide, 3–4.5 mm. long, with body from ovoid to lanceoloid, bi-convex to plano-convex, the base stipitate, greenish-brown to brown, chartaceous-membranous, strongly 9–12-nerved on a side, rostrum one fourth as long as the body, often minutely toothed on the upper third, bidentate, teeth 0.5–0.8 mm. long; achenes lenticular, minutely rugose in longitudinal lines, light brown to greenish; style and stigma 3 mm. long, stigmas two, 2 mm. long, minutely glandular, dark brown.

Distribution: On all islands in Zone D of Ripperton and Hosaka (1942), or middle forest between 600 feet and 3,500 feet on ridges in full sun or in dense shade and on moist rocky ravine walls. Optimum development in semi-shade.

Type: F. J. F. Meyen, in Oahu Insula Sandvicensium, June, 1831. The specimen is with the Meyen plants in the herbarium at Leningrad. Requests for the loan of plants from Leningrad were unanswered.

Specimens examined

KAUAI: *Faurie 1201,* Waimea, 1000 m., Mar. 1910, (KY); *Fosberg 12673,* head of Kalalau Valley, 1250 m., Dec. 29, 1935; *Mann & Brigham 391,* Waimea, 2000–3000′, (C); *Nuttall,* Kauai (no data), (K); *Nuttall,* Kauai (no data), 1843, (K); *St. John 22902,* Kilauea Lookout, Kalalau Valley, 4000′, Dec. 21, 1947.

OAHU: *Degener 19412,* N slope of Mt. Kaala, Feb. 2, 1949, (NY); *Faurie 1209,* Honolulu, Apr. 1909, (GB); *Faurie 1211,* Kaala, Nov. 1909, (KY); *Forbes 2465.O,* ridge between Niu and Wailupe, Apr. 11, 1917; *Forbes 2525.O,* Wailupe, Jan. 1919; *Fosberg 10893,* head of Makaha Valley, S side, 1500′, Mar. 31, 1935, (US); *Fosberg 13040,* head of Kapuna Valley, Mokuleia, 600 m., Apr. 11, 1936; *Fosberg 13602,* head of Kawaihapai Gulch, Feb. 21, 1937; *Fosberg 13005,* E ridge of Puu Kalena, 950 m., Mar. 22, 1936; *Fosberg 13631,* N ridge of Puu Kumakalii, Mar. 28, 1937; *Gaudichaud,* near Honolulu and the Pali, 1836, (K); *Judd & Hosaka,* Pahaia Valley, sixth valley E of Makaliha, 1200′, Dec. 2, 1931; *Krauss 122,* trail to Puu Kaua, 1800′, Feb. 29, 1948; *Krauss 119,* trail to Puu Kaua, 1700′, Feb. 29, 1948; *Krauss 137,* Papoli ridge above Maakua, 600′, Mar. 21, 1948; *Krauss 141,* Papoli ridge above Maakua, 450′, Mar. 21, 1948; *Krauss 148,* third ridge N of Palikea,

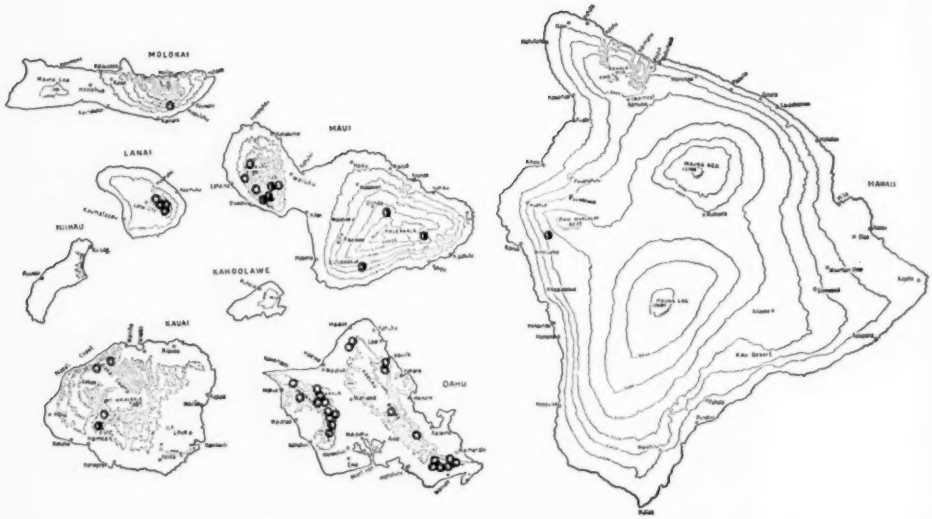

FIG. 9. Distribution of *Carex Meyenii* Nees.

W side, 2000′, Mar. 26, 1948; *Krauss 300,* summit of Kuliouou Trail, Aug. 6, 1948; *Krauss 299,* below summit of Kuliouou Trail, Aug. 6, 1948; *Krauss 298,* below summit of Kuliouou Trail, Aug. 6, 1948; *Krauss 291,* Kuliouou Trail, 1200′, Aug. 6, 1948; *Krauss 290,* Kuliouou Trail, 1200′, Aug. 6, 1948; *Krauss 317,* Palolo Trail to Kaau Crater, 1400′, Aug. 13, 1948; *Krauss 557,* Stream bed of Elehaha, 500′ from Road, 850′, Apr. 16, 1948; *Mann & Brigham 260,* Waialua Mts., (C); *Remy 141,* 1851–55, (GH, P); *St. John 11026,* Kipapa Gulch, second N fork, Waipio, 1300′, Feb. 15, 1937; *St. John 10382,* N fork of valley E of Palikea, 1300′, Feb. 23, 1930; *St. John 13156,* Pohakea Pass, 2200′, May 12, 1933; *St. John 14037,* E ridge of Puu Kanehoa, 2400′, Jan. 7, 1934; *Skottsberg 44,* Keawaawa, Aug. 4, 1922; *Wilkes Exped.,* Honolulu, 1838–42, (US).

MOLOKAI: *Faurie 1207,* Kamalo, June 1910, (KY); *Forbes 361,* Kaluaaha Valley, Aug. 1912.

LANAI: *Fagerlind & Skottsberg 6767,* summit of main ridge in wet forest, Apr. 2, 1948, (GB); *Fagerlind & Skottsberg 6419,* NW part of main ridge, Feb. 25, 1948, (GB); *Fosberg 12480,* ridge below Puu Aalii between Maunalei drainage and Hauola drainage 2600′, Nov. 30, 1935, (US); *Hitchcock 14666,* on largest mountain, Sept. 21, 1916, (US); *Munro 155,* ridge above Hookio, Oct. 11, 1913; *Munro 451,* Hookio, Oct. 6, 1913; *Rock 8083,* Mahana, July 25, 1910; *St. John 18705,* Puu Ealii, Kealia Aupu–Kaunolu, 2700′, Apr. 9, 1938.

MAUI: *Forbes 320.M,* Lahainaluna Valley, Feb. 19, 1913; *Forbes 2391.M,* Olowalu Valley, May 17, 1920; *Forbes 2047.M,* Kalualii, middle Auwahi, Mar. 20, 1920; *Forbes 2406.M,* Olowalu Valley, May 17, 1920; *Forbes 699.M,* NE of Ukulele, July 9, 1919; *Hitchcock 14961,* Haleakala crater, 6000–10,000′, Oct. 2–5, 1916, (US); *Hitchcock 12900,* Haleakala, 6000–10,000′, Oct. 2–5, 1916; *Krauss 464,* confluence of Honokawai and Waikiki, Sept. 11, 1948; *Rock 8752,* Waikahu Valley, 900′, May 1911; *St. John & Catto 17613,* S ridge of Launiupako Valley, 2550′, Dec. 20, 1936.

HAWAII: *Skottsberg 631,* slope of Hualalai, 1200 m., Sept. 23, 1922.

Carex Meyenii Nees belongs to the subgenus *Eucarex,* Coss. & Germ., section *Hymenochlaenae,* Drejer (Kükenthal 1909; 576), subsection *Graciles,* Tuckerman (Kükenthal 1909: 599). The subsection is widespread in the Pacific from South America to the center of Asia. The Hawaiian plant has been described as *Carex Remyi* by Boeckeler, as *Carex Meyenii* by Nees, and, in part, as *Carex Commersoniana* by Kunth, all believing it to be a distinct species. *Carex Commersoniana* Kunth is described with "Sieb herb. Maurit. no. 50" cited as the type immediately following the binomial. However, after the description, *Carex Meyenii* of Nees is cited as a juvenile specimen of *Carex Commersoniana.* Kunth's description does not fit the Hawaiian plant, nor does Plate 155 of F. Boott in *Illustrations of the Genus Carex,* which was drawn from Mauritian material. There is no question that Kunth is naming the plant now known as *Carex brunnea* Thunb. under which Kükenthal cites Sieber herb. Maurit. no. 50. *Carex Commersoniana* Kunth is a later homonym of *Carex brunnea* Thunb. and cannot be applied to the Hawaiian species. Hillebrand (1888: 489) describes it as a new variety, β, of *Carex brunnea* based on *Mann & Brigham 391.* Kükenthal also describes it as a variety of *Carex brunnea.*

Authentic specimens of the Japanese *Carex brunnea* Thunb. were secured from the University of Kyoto, Japan. They are not the same species as the Hawaiian plant though they do clearly belong to the same subsection. The differences are pronounced. The perigynia in the Hawaiian plants are lanceolate with long tapering rostra. Those in the Japanese material *(Faurie 4945)* are broadly ovate to circular in outline with an abrupt narrow rostrum. Further, the surface of the perigynia in the Japanese material is strongly hispid with prominent white hairs. The Hawaiian perigynia have only setae on the margins. The bracts in the Japanese specimens are broad ovate; those in the Hawaiian ones are much narrower.

The perigynia, in fact, more closely approach those in the Chinese *Carex longicruris* Nees. However, the long stigmas and the extreme branching spikes as well as the greater size in the latter make it a remote member of the subsection.

Carex Meyenii Nees is found on all the main islands but seems to have its center of distribution in the west, indicating a center of dispersion from either Kauai or Oahu.

Carex Nealae sp. nov.

Figs. 10*a–c,* 11

Rhizomatis distinctis lignosis caespitosis in apicibus, squamis radicibus 4–6 mm. latis 1–4 cm. longis 2–5 in culmis caducis, culmis 1.5–2 mm. latis 30–45 cm. longis erectis triangulis striatis glabris fuscis, laminis 4–5 mm. latis 15–50 cm. longis 3–10 in culmis saepe ad apicem compressis inflorescentiis excedendis marginibus superioribus scabris inferioribus glabris, vaginis membranis hyalinis clausis laminis culmibusque in fasciculo tenendis, inflorescentiis 3–4 mm. latis 4–6 cm. longis ramosis nodis 1–5 spiciferis 1–5 nodis, internodis inferis 1–2 cm. longis supris brevioribus, nodis bractis laminiferis inclusis, spicis 3–4 mm. latis 1.5–5 cm. longis androgynis praeter terminalis masculis multifloribus, pedunculis 3–5 mm. longis includendis in ocresis bipartitis in apicibus purpureimaculosis, squamis foeminis 1.4 mm. latis 2.5 mm. longis ovatis emarginatis cum costa alba interdum breve aristatis brevis marginibus hyalinis rubris aut purpureis, squamis masculis 1.5 mm. latis 5 mm. longis lanceolatis emarginatis costa alba in marginibus rubris aut purpureis, utriculis 1.5–2 mm. latis 3–4 mm. longis ovoideis aut latis ovoideis stipitatis valde 5–6 nervosis fuscis cum glandibus rubris maculosis, rostris brevibus apicibus integribus, achaenis obovoide biconvexis rugosis fuscis, stylis in duo stigmatis glandulosis 2–3 mm. longis divisis.

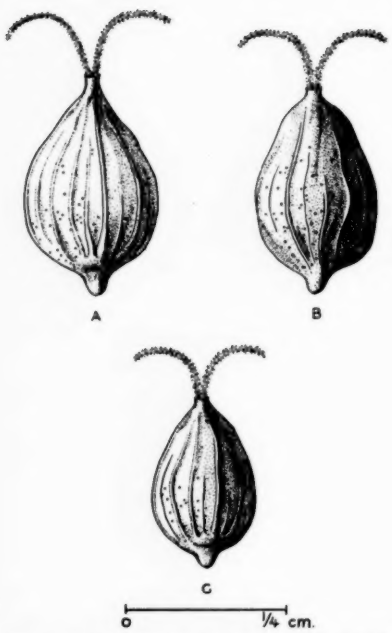

FIG. 10. Perigynia of *Carex Nealae* R. Krauss. *a, Forbes 1187.M; b, Forbes 1191.M; c, Neal and Hartt 698.*

Rhizome distinct, branching, lignescent, becoming caespitose at the apex; basal scales 4–6 mm. wide, 1–4 cm. long, brown, fibrillose, 2–5 per culm, caducous; fertile culm, 1.5–2 mm. wide, 30–45 cm. long, triangular in cross section, erect, stiff, striate, smooth on the angles, brown; leaves 4–5 mm. wide, 15–50 cm. long, slender, erect, 3–10 per culm, V-shaped, often folded to the apex, long, tapering, usually exceeding the inflorescence, sparely scabrous on the upper margins, smooth below; sheaths closed by a hyaline membrane splitting almost at inception, holding culms and leaves in slender bundles 9–15 cm. above the base, dark brown; inflorescence 3–4 mm. wide, 4–6 cm. long, apical, erect, branching, one spike per node, 1–5 nodes per inflorescence, lower internodes 1–2 cm. long, the upper shorter, each node enclosed by a leafy bract, the lower 10–15 cm. long, the upper shorter; spikes 3–4 mm. wide, 1.5–5 cm. long, androgynous except the terminal spike which is staminate, densely flowered, peduncles 3–5 mm. long, enclosed by a split ochrea 1–2 mm. long, purple-spotted at the apex; pistillate bracts 1.5 mm. wide, 2.5 mm. long, ovate, predominantly strongly emarginate with a single white dorsal nerve sometimes extending into a short awn, margins hyaline, red to purple; staminate bracts 1.5 mm. wide, 5 mm. long, lanceolate, emarginate, white along dorsal nerve, red to purple in margins; perigynia 1.5–2 mm. wide, 3–4 mm. long, ovoid or broadly so, bi-convex, short stipitate, strongly 5–6-nerved, brown, chartaceous, numerously spotted with reddish glands; rostrum tapering to an entire apex, achenes obovoid, bi-convex, more convex on one side than the other, minutely rugose, dark brown; style splitting into two spreading stigmas at the apex of the rostrum, stigmas 2–3 mm. long, glandular.

Distribution: Hawaii and Maui in Zones D and E of Ripperton and Hosaka (1942), the middle and upper forest, growing in bogs and pools in pahoehoe lava in full sun, rare.

Type: Forbes 1191.M, Waianapanapa, at edge of lake, Haleakala, Maui, Aug. 20, 1919.

Specimens examined

MAUI: *Forbes 861.M,* East of Ukulele, July 20, 1919; *Forbes 1187.M,* Waianapanapa, Haleakala, Aug. 20, 1919; *Forbes 1191.M* (See Type).

HAWAII: *Neal M., and Hartt, C., 698,* East of Humuula below Kalaeeha in pool, 6200′, Aug. 7, 1935.

Carex Nealae belongs in subgenus *Eucarex* Coss. & Germ., section *Acutae* Fries subsection *Vulgares* Aschens (Kükenthal 1909: 305). It has unquestioned Australian relationships, being close to *Carex Gaudichaudiana* Kunth, which grows in bogs in the mountains of New South Wales and New Zealand. It differs from this species, how-

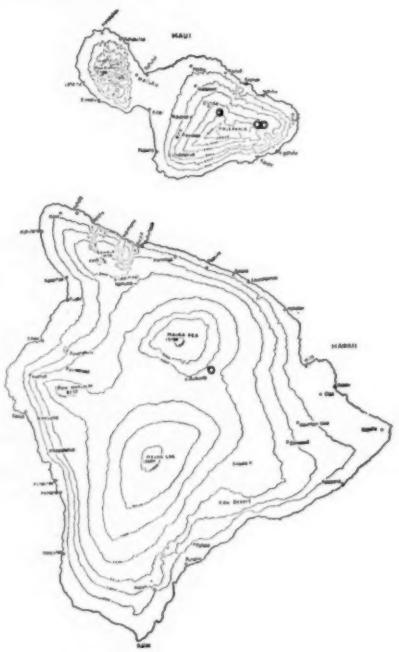

FIG. 11. Distribution of *Carex Nealae* R. Krauss.

ever, in several respects. In *Carex Nealae* the pistillate bracts are predominantly strongly emarginate and the margins are reddish-purple and opaque. In *Carex Gaudichaudiana* Kunth the pistillate bracts are all obtuse, and are light brown with hyaline margins. The spikes in *Carex Nealae* are 4–5 cm. long; those of *Carex Gaudichaudiana* Kunth are semi-globose, reaching only 2 cm. in length. The margins of the narrower leaves of *Carex Gaudichaudiana* Kunth are involute; those of *Carex Nealae* are not.

The species is named out of respect for Miss Marie Neal of the Bernice P. Bishop Museum Herbarium, who collected the plant on Hawaii in 1930.

The distribution of *Carex Nealae,* at present collected only four times, suggests that it is to be found at the edges of stagnant water at elevations over 3,000 feet. However, the vegetation need not be primarily bog type.

Carex macloviana D'Urv. (1826: 599) var. **subfusca** (W. Boott) Kükenth. Engler's Pflanzenreich, IV: 20, 197, Pl. V, 1909. Figs. 12*a–c*, 13

Carex subfusca W. Boott. In: Botany of California 2:234, 1880.

Rootstocks caespitose, forming small clumps 15–20 cm. in diameter; basal scales two to four, 2–3 mm. wide, 1–5 cm. long, persistent, brown; fertile culm triangular in cross section, sides 0.6–1 mm. wide, 15–60 cm. long, strongly ribbed, scabrous on the angles, pendent, leaves 1–2 mm. wide, 10–70 cm. long, narrow, scabrous along midrib and margins, pendent, dark green; sheaths tightly closed by a chartaceous to hyaline membrane which splits almost at once to 10 cm. above the rootstock, brown; inflorescence forming ovoid to cylindric head, 0.8–1 cm. wide, 1–2 cm. long, densely flowered, 4–9 spikes closely spirally arranged at the apex of the culm, internodes 1–2 mm. apart, each spike subtended by a bract, the lower leaf-like to 1 cm. long, the upper scale-like; spike gynaecandrous, 2–3 mm. wide, 5–6 mm. long, sessile, subtended by a leafy bract or scale which may have stipule-like appendages; pistillate bracts, 1.5–2 mm. wide, 3 mm. long, obovate acute to acuminate, with minute teeth on the keel near the apex, membranous, brown with a green keel; staminate bracts similar; perigynia 1.5–2 mm. wide, 3–4.5 mm. long, narrowly lanceoloid, long, tapering to the apex, narrowly winged, strongly concave-convex, faintly several-nerved on each side or not nerved, chartaceous, brown to green, wing toothed on the margins, rostrum grooved on the convex side, deeply bidentate on the convex side, shallowly bidentate on the concave side; achenes ovoid, bi-convex, stipitate, surface shining golden, minutely punctate; style 1.5–2 mm. long, splitting at half its length into two glandular stigmas.

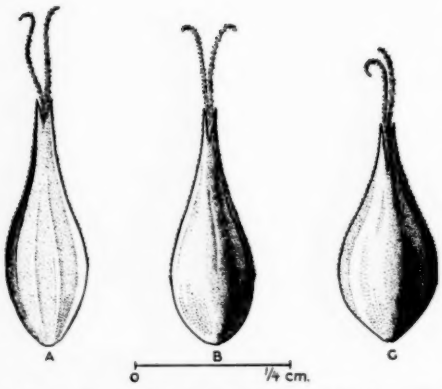

FIG. 12. Perigynia of *Carex macloviana* var. *subfusca* (W. Boott) Kükenth. *a, b, Forbes 719.M; c, Giffard* in 1911.

Distribution: Hawaii and Maui, in Zones D and E of Ripperton and Hosaka (1942), the upper forest, in dry, sunny meadows or grassy ravines, usually over 5,000 feet.

Type: Kellogg, Lake Tahoe, Bear Camp, Cal. (GH); from Herbarium of William Boott.

Specimens examined

MAUI: *Cranwell, Selling, Skottsberg 2794,* Haleakala, 2200 m., Aug. 4, 1938, (GB); *Degener,* Koolau Gap, June 29, 1929, (NY); *Degener 9014,* Mauka of Ulupalakua, July 4, 1927, (NY); *Degener 9013,* Slope of Haleakala, Aug. 10, 1927, (NY); *Degener 9011,* Pipe Line, Olinda, June 14, 1927, (NY); *Degener 9015,* Koolau Gap, Haleakala, Aug. 19, 1927, (NY); *Degener 9012,* Koolau Gap, Haleakala, June 29, 1927, (NY); *Faurie,* Haleakala Crater, Aug. 11, 1909; *Forbes 1248.M,* Kaupo Gap, Haleakala, Aug. 25, 1919; *Forbes 719.M,* E of Ukulele, July 11, 1919; *Forbes 975a.M,* Pasture above Ukulele, July 29, 1919; *Forbes 1010.M,* Kaeanae Gap, Halekaku, Aug. 2, 1919; *Forbes 1099.M,* Haleakala, Kaupo Gap, Aug. 9, 1919; *Forbes 1186.M,* N slope of Haleakala, Waianapanapa, Aug. 20, 1919; *Forbes 1227.M,* Bog below Waianapanapa, Aug. 25, 1919; *Hitchcock 14977,* Haleakala, 6–10,000′, Oct. 2, 1916; *Krauss 350,* Switchback Trail above Holua, 8000′, Sept. 3, 1948; *Krauss 355,* Draw behind Paliku, 6800′, Sept. 2, 1948; *Krauss 343,* half mile N of Paliku, 7000′, Sept. 3, 1948; *Krauss 341,* half mile N of Paliku, 7000′, Sept. 3, 1948; *St. John 17776,* Haleakala Crater, Cinder Flat, 7000′, Dec. 26, 1936; *Skottsberg 830,* Haleakala, inside crater, W side, 2200 m., Oct. 16, 1922.

HAWAII: *Degener 9009,* Kipuka Puaulu, Kilauea, May 1932, (NY); *Degener 9010,* Kau Desert, 10 M. from Volcano House, June 16, 1929, (NY); *Faurie 1219,* Mauna Kea, 2000 m., July 1909; *Faurie 1220,* Mauna Kea, 2000 m., July 1909; *Faurie 1218,* In Kilauea Volcano, May 1909; *Forbes,* Kona, Hanehane, June 15, 1911; *Forbes 177.H,* Hualalai above Hanehane, June 16, 1911; *Forbes 306.H,* Mauna Loa

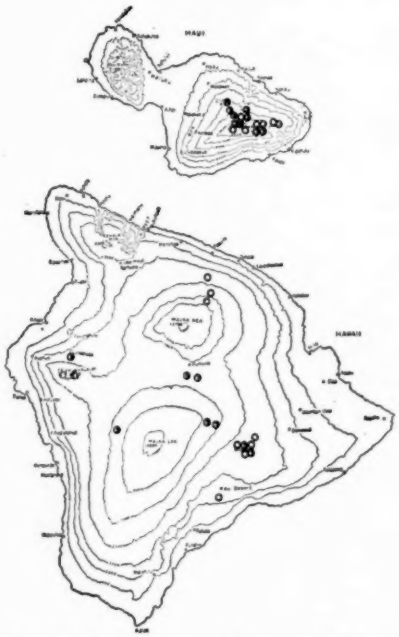

FIG. 13. Distribution of *Carex macloviana* var. *subfusca* (W. Boott) Kükenth.

below Pui-o-Uo, July 11, 1911; *Forbes 972.H,* Flow of 1823, Level of Keawewai, June 28, 1915; *Giffard,* Kilauea Volcano, June 1911; *Hapeman,* Volcano House, Kilauea, Apr. 23, 1908, (NY); *Hitchcock 14528,* Hualalai Mt., Sept. 2, 1916, (US); *Hitchcock 14238,* Kukaiau Ranch, 8000′, Aug. 21, 1916, (US); *Hitchcock 14226,* Kukaiau Ranch, 3600′, Aug. 20, 1916, (US); *Hitchcock 14317,* Maunakea, NE slope, 7000′, Aug. 23, 1916, (US); *Mann & Brigham 332,* high central plateau of Hawaii; *Remy 146,* 1851–55, (GH); *Rock 12731,* Kilauea Volcano, July 1911; *St. John 11438,* Puu Hualalai, Kaupulehu, summit of volcanic cone, 8000′, Dec. 30, 1931; *Skottsberg 524b,* E slope of Mauna Loa, Sept. 15, 1922, (GB); *Skottsberg 570,* Kilauea, Tree Fern Forest, Sept. 17, 1922, (GB); *Skottsberg 494,* Kilauea, crater trail, Sept. 12, 1922, (GB); *Skottsberg 524,* Trail to rest house, Mauna Loa, Sept. 15, 1922, (GB); *Wilkes Exped.,* 1838–42, (US).

Carex macloviana, in the subgenus *Vignea* (P. Beauv.) Nees (Kükenthal 1909: 111) section *Ovales* Kunth (Kükenthal 1909: 191), is a widespread and confusing species. Kükenthal has described 10 varieties and forms corresponding more to geographical regions than to characters. Specimens of a number of these varieties have been examined. They represent collections from California, Colorado, and Nevada in the United States, and from the Falkland Islands, Mexico, Greenland, Kamchatka, Canada, Unalaska, Sweden, and Chile.

The Hawaiian species show a clear relationship to the varieties *subfusca* (W. Boott) Kükenth. and *pachystachya* (Cham.) L. H. Bailey. They do not seem to be close to the varieties from South America which have perigynia which are more broadly winged, more strongly nerved, and less concave-convex in cross section. The latter include the type for *macloviana* sent from Santiago, Chile.

In my opinion many of the varieties of *Carex macloviana* D'Urv. represent differing biotypes with neither ecological nor genetic basis for their segregation. In specimens of the Hawaiian plant a clear gradation may be observed, often in the same inflorescence, from perigynia strongly nerved to not nerved, from strongly squarrose to not squarrose, etc.

The type collection of Kellogg from California has been examined. It corresponds very closely to the Hawaiian plant. It is not possible, without more material, to determine if *Carex subfusca* W. Boott is a good species. The world distribution of *Carex macloviana* D'Urv., and the slight differences in its population, prevent the retention of *Carex subfusca* W. Boott as a Linnaean species; however, its varietal status appears to be sound.

Carex pluvia sp. nov.

Figs. 14*a–c*, 15

Carex sandwicensis Boeckler (1875: 265) var. *laxiflora* Kükenth. Fedde Rep. XVI, 435, 1920.

Rhizomatis caespitosis in glaebis laxis 30 cm. in diametrio, squamis radicorum 7–8 mm. latis 1–5 cm. longis fibrillosis, culmis fertilibus 2–3 mm. latis 45–75 cm. longis erectis triangularibus concavis striatis glabris apicibus caulorum pendulis, 6–10 laminis 5–7 mm. latis 15–75 cm. longis pendulis culmis fertilis raro excedendis in marginibus saepe revolutis scabris in apice glabris in basi vaginis laxis membranace evanescendentibus clausis, inflorescentis ramosis pendulis aut erectis 8–10 nodis unispiciferis pedunculis et ocreis in laminis-bracteis inclusis inflorescentiis excedendis, spicis 3–5 mm. latis 3–9 cm. longis multifructibus androgynis praeter spicis terminalis masculis, pedunculis in ocreis inclusis et squamis sterilis ocreis superioribus, squamis foeminis 1 mm. latis 4 mm. longis lanceolatis in centris triplinervosis ovatis acuminatis marginibus hyalinis fulvis, squamis

masculis 0.5 mm. latis 4–5 mm. longis 2–3 nervosis, utriculis 1–1.5 mm. latis 2–4 mm. longis ellipsoideis aut ovoideis aut ovatis-ellipsoideis, chartaceis fulvis enervosis aut trinervosis, breve stipitatis rostris bidentatis marginibus incrassatis raro setaciferis, achaenis lenticularibus rugosis fulvis utriculis non complentibus, stylo 0.5–1 mm. longo erecti.

Rootstocks caespitose, forming loose clumps 30 cm. in diameter; basal scales 7–8 mm. wide, 1–5 cm. long, fibrillose; fertile culm 2–3 mm. wide, 45–75 cm. long, triangular in cross section, faces concave, erect, stiff, nodding only at the ends, striate, smooth; leaves 5–7 mm. wide, 15–75 cm. long, 6–10 per culm, pendent, slender, seldom exceeding the fertile culms, V-shaped in cross section, revolute at the margins, tapering, scabrous at the ends, smooth toward the base, light green; sheaths 3–8 cm. long, closed by a very thin rapidly disappearing membrane, loose, light brown; inflorescence pendent to semi-erect, branching, 8–10 nodes, one spike to a node, each node and ochrea bearing peduncle enclosed in a leafy bract exceeding the inflorescence by 1–10 cm.; spikes 3–5 mm. wide, 3–9 cm. long, androgynous except the terminal spike which is staminate, closely set with fruit, pedunculate, peduncles enclosed by an ochrea, several sterile scales above the ochrea; pistillate bracts 1 mm. wide, 4 mm. long, lanceolate to ovate, acuminate, triple-nerved in the center, green to yellow, margins hyaline, brown to red; staminate bracts lanceolate, 0.5 mm. wide, 4–5 mm. long, 2–3-nerved at the center; perigynia 1–1.5 mm. wide, 2–4 mm. long, ellipsoid, varying to ovoid or even obovoid-subspherical, chartaceous, yellow to brown, short stipitate, not nerved or with as many as three nerves, rostrum bidentate, margins ridged, occasionally armed with large, caducous setae; achenes lenticular, rugose, not filling the perigynia, yellow to brown; style erect, 0.5–1 mm. long, splitting into two glandular stigmas at the apex of the rostrum.

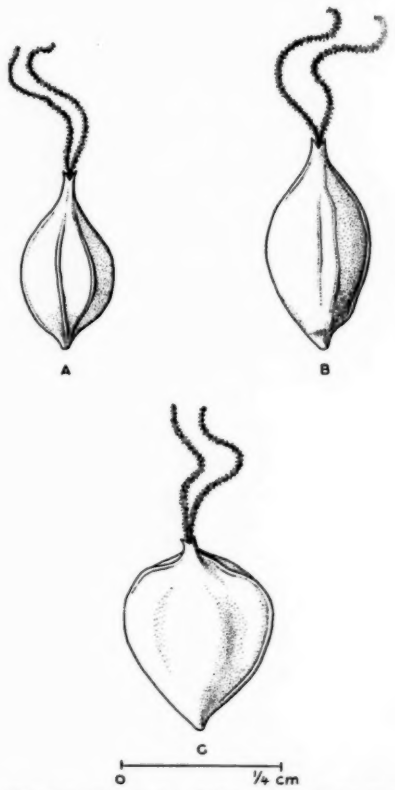

FIG. 14. Perigynia of *Carex pluvia* R. Krauss. *a, Krauss 218; b, Fosberg 13757; c, Krauss 415.*

Distribution: On all the islands, except Lanai, in Zone D_2 of Ripperton and Hosaka (1942), the middle forest, in very wet, shady places; often in the beds of streams or in the water.

Type: Krauss 218, In Kaluanui Stream among rocks beside rapidly flowing water, 1,950 feet, May 23, 1948.

Specimens examined

KAUAI: *Faurie 1202,* Waimea, 1000 m., Feb. 1910 (immature?); *Hitchcock 15328,* Kaholuamano, Mar. 3, 1901, (US); *Rock 1665,* Kaholuamano, Mar. 3, 1909; *Rock 5042,* Kaholuamano, Sept. 1909; *Smith, Whitney, Neal,* Kokee, 3500′, May 1, 1929;

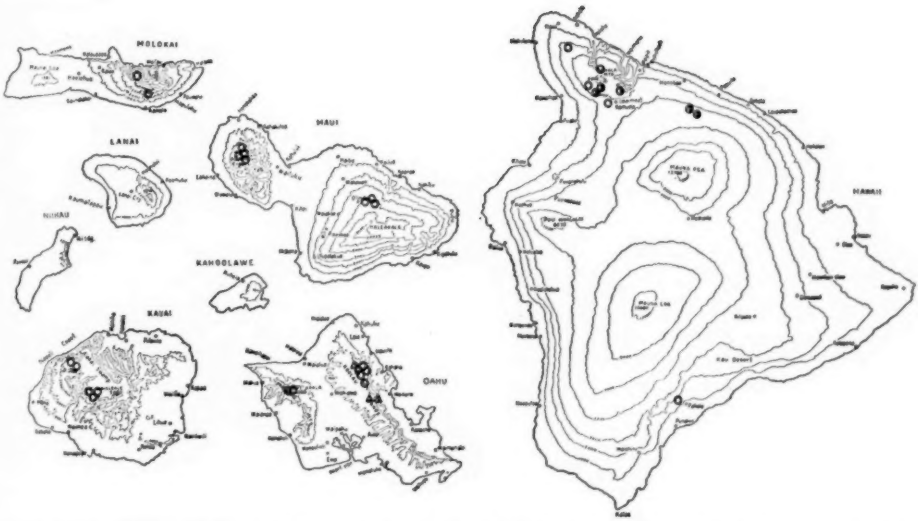

FIG. 15. Distribution of *Carex pluvia* R. Krauss (indicated by circles) and of *C. pluvia* var. *koolauensis* R. Krauss (indicated by triangles).

Wilder 450, Kokee Stream, 3600′, Mar. 8, 1926.

OAHU: *Christophersen 1747,* top of Kaala, 1200 m., May 10, 1931; *Forbes & Clark,* between Punaluu and Kaipapau, May 3, 1909; *Fosberg 13680,* Puu Kaala summit, W side, Mar. 24, 1937; *Fosberg 13757,* Kaluanui Valley, 600 m., Apr. 25, 1937; *Krauss 224,* In Kaluanui Stream, 1950′, May 23, 1948; *Krauss 208,* In Kaluanui Stream, 1950′, May 23, 1948; *Krauss 209, 210, 211, 212, 213, 214, 215, 216, 217,* and *218* same data as *208; Krauss 505,* in bed of Kaluanui stream, 1950′, Nov. 21, 1948; *St. John & Cottam 23556,* Poamoho Stream, 2000′, Feb. 20, 1949.

MOLOKAI: *Degener 8236,* S of Ohialele, May 8, 1928, (NY); *Hitchcock 15094,* North of Kamalo, 4000′, Oct. 10, 1916, (US).

MAUI: *Degener 8251a,* Stream bed, Olinda Pipe Line, June 16, 1927, (NY); *Degener 8248,* Oohuola stream-bed near ditch trail, July 7, 1927, (NY); *Forbes 1257.M,* Kula Pipe Line, Waikamoi, Sept. 5–6, 1919; *Forbes 2602.M,* Waikamoi Trail, June 25, 1920; *Forbes 580.M,* E of Ukulele, July 15, 1919; *Fosberg 10040,* Puu Kukui, pool, 1700 m., Aug. 24, 1933; *Hitchcock 15094,* N of Kamalo, 4000′, Oct. 10, 1916, (US); *Krauss 480,* trail above Haelaau, Puu Kukui, 5000′, Sept. 12, 1948; *Krauss 380,* Olinda Flume Line trail, 4300′, Sept. 6, 1948; *Krauss 473,* trail above Haelaau, Puu Kukui, 5000′, Sept. 12, 1948; *Krauss 381,* stream bed above Olinda trail, 4300′, Sept. 6, 1948; *Krauss 409,* trail above Haelaau, Puu Kukui, 4800′, Sept. 8, 1948; *Krauss 415,* trail above Haelaau, Puu Kukui, 4500′, Sept. 8, 1948; *Krauss, 427,* trail above Haelaau, Puu Kukui, 4800′, Sept. 8, 1948; *Rock 8751,* Olinda Waikamoi, Apr. 22, 1911.

HAWAII: *Cranwell 3456,* Kohala Mts. near Kamuela, Sept. 29, 1922, (GB); *Degener 2216,* 17 mi. from Kohala to Waimea, June 31, 1926, (NY); *Degener 2212B,* 17 mi. from Kohala to Waimea, June 31, 1926, (NY), (mixed collection); *Faurie 1215,* Glenwood, May 1907, (KY); *Forbes 501.H,* Kohala Mts., Waimea, Sept. 1911; *Rock*

3170, Paauhau, June 24, 1909; *Rock 3173,* Paauhau No. 1 Stream, 3000′, June 24, 1909; *Skottsberg 705,* Kohala Mts. near Kamuela, Sept. 29, 1922, (GO); *Skottsberg 593,* S slope of Mauna Loa above Pahala, Sept. 19, 1922, (GO).

Carex pluvia R. Krauss, a member of subgenus *Eucarex,* section *Acutae* Fries, subsection *Cryptocarpae* Tuckerman (Kükenthal 1909: 297), stands close to *Carex alligata* F. Boott. It differs from the latter in the dull membranous to chartaceous bi-convex perigynia, which may bear setae on the rostrum and on the rostrum base, as in *Forbes 501.H* and *Forbes 580.M.* It is often 1–3-nerved from the stipitate base. This species is related to *Carex laciniata* F. Boott. It differs from *Carex laciniata* F. Boott primarily in the lack of the multiveined perigynia and in the more clearly bidentate rostrum; also, the peduncles are shorter and the internodes in the inflorescence are much reduced in *Carex pluvia.* It is usually of smaller stature, about 50 cm. long, rarely reaching 75 cm. Certain specimens have been collected with the intact spikes bearing hundreds of germinated seeds *(Krauss 380).*

The placing of the group as a species seemed at first to be questionable. Inasmuch as *Carex pluvia* and *Carex sandwicensis* were found growing together, especially on Maui, the possibility of wide biotypic variation seemed great. However, the plants growing in the same general areas seemed to have ecologic preferences, *Carex pluvia* in the wet shaded areas, often in running water, and *Carex alligata* in the drier sunny uplands. This suggested that they might be ecologic forms or varieties, but the distinctness of shape and surface of the perigynia, verified by repeated visits to the same plants as they matured, and the lack of intermediate forms between the two, although growing side by side, seem to eliminate this possibility. The distribution also gives some clue as to the constancy of the species. *Carex pluvia* is found alone on Oahu and together with *Carex alligata* on Maui, Hawaii, and Kauai.

In spite of its distinguishing characters the species is probably a recent one. The differences within the specific limits, especially the occurrence of extremely large though caducous setae on the ridge running into the rostrum, are remarkable and would suggest another species to many taxonomists.

Carex laxiflora Lam is an earlier name applied to a different plant; therefore maintaining the epithet of the variety of Kükenthal would create a later homonym. The epithet *pluvia* suggests the habitat in and along watercourses subject to flooding. It is the Latin adjective *pluvius,* meaning wet or rainy.

Carex pluvia var. ***koolauensis*** var. nov.

Figs. 15, 16*a–b*

A specie differt in squamis radicorum 8–12 mm. latis 1–11 cm. longis crassis persistentibus rubris aut purpureis culmis fertilibus 2–4 mm. latis, 50–100 cm. longis erectis striatis, in apicibus scabris ad basim glabris, laminis viridibus sed ad basim, rubris aut purpureis vaginis lignosis rubris aut purpureis, inflorescentis 8–15 cm. longis erectis ramosis 7–11 nodis 103 spiciferis, internodis inferis 2–3 cm. longis superioribus brevioribus, bractis-laminiferis inferioribus 30–45 cm. longis superioribus brevioribus, pedunculis 3–7 mm. longis in ocreis purpureis lanceolatis inclusis, squamis foeminis utriculis aequantibus carinis dorsalibus 2–3 albi-nervosis in marginibus membranaecis purpureis, utriculis 1–2 mm. latis 3–4 mm. longis incrassatis striatis ovoideis aut anguste oblongi-ovoideis purpureis-nigris fulgentibus stipitatis rostris 1 mm. longis bidentis, achaenis biconvexis obovoideis utriculis semi-complentibus rugosis aut glabris aureis.

Differs from the species in the following characters: basal scales 8–12 mm. wide, 1–11 cm. long, coarse, persistent, shiny, red to

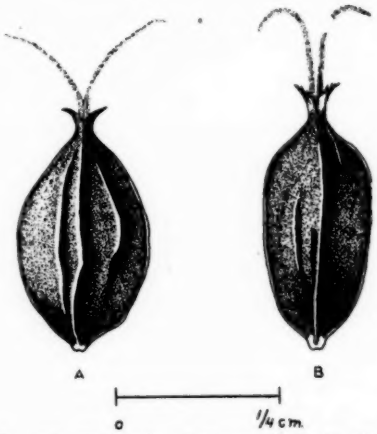

FIG. 16. Perigynia of *Carex pluvia* R. Krauss var. *koolauensis* R. Krauss. *a, Hosaka 594; b, St. John 17978.*

purple; fertile culm 2–4 mm. wide, 50–100 cm. long, erect, striate, scabrous on the angles above, smooth below; leaves brilliant red to purple at the base, light green above; sheaths ligneous, brilliant red to purple; inflorescence 8–15 cm. long, erect, branching, 1–3 spikes to a node, 7–11 nodes to an inflorescence, the lower 2–3 internodes 2–3 cm. long, the upper much shorter forming a dense head, each node enclosed by a leafy bract, the lower 30–45 cm. long, the upper shorter; peduncles of spikes 3–7 mm. long, enclosed by a purple, lanceolate ochrea; pistillate bracts equalling the perigynia, 2–3 white nerves along the dorsal keel, margins membranous, purple; staminate bracts lanceolate, 2–3 white nerves along the keel, margins membranous, purple; perigynia 1–2 mm. wide, 3–4 mm long, ridged, ovoid or narrowly oblong-obovoid, 1–3 ridged or veined, shiny, purple to black, rostrum 1 mm. long, bidentate, stipitate; achenes bi-convex, obovoid, filling only half of the perigynium, rugose to smooth, yellow.

Distribution: Oahu in Zone D_2 of Ripperton and Hosaka (1942), the middle forest, in wet areas in turf; usually with grasses.

Type: Hosaka 594, Kipapa Gulch, 2,500 feet, July 4, 1932.

Specimens examined

OAHU: *Fosberg 9730,* Kipapa Gulch, 850 m., Aug. 6, 1933; *Fosberg and Hosaka 13946,* head of Kawaiiki Gulch and Kaluanui Gulch, 900 m., May 30, 1937; *Hosaka 594* (see type); *St. John 17978,* Hauula, Castle Trail, 2500′, Apr. 25, 1937; *Takata,* Castle Trail, Kaluanui, 1000′, Apr. 25, 1937.

The variety *koolauensis* was first found by Edward Hosaka in 1932. It has been collected since in two other stations on Oahu. The variety shows transition with the species in *Fosberg and Hosaka 13946* in that the purple-black covering of the perigynia is fully formed in some and just beginning to form in others. The perigynia are characteristically more narrow and more strongly stipitate than those of the species. The two teeth of the beak are longer and more conspicuously divaricate. With the small number of collections it seems unwise to classify the population as a new species, though its appearance is considerably different. Its rarity, in turf in regions well populated by the species, suggests the possibility that it is a variation resulting from an unusual combination of minor genetic differences as well as of ecological extremes.

Carex alligata F. Boott, Illust. Genus Carex IV, 129, 1867.

Figs. 17*a–f*, 18

Carex sandwicensis Boeckler, Flora, 265, 1875.

Carex crustacea Nelmes, Kew Bull. I, 11, 1946.

Rootstocks caespitose; basal scales 8–15 mm. wide, 3–12 cm. long, 3–6 per culm, fibrillose, brown to purple; fertile culm triangular in cross section, 3–4 mm. wide, 60–150 cm. long, erect, striate, scabrous on the angles above, becoming smooth below; leaves 8–15 mm. wide, 20–120 cm. long, 4–8 per fertile culm, erect below, pendent above, V-shaped to flat, shiny, scabrous on the main

veins and margins, tapering, dark green; sheaths 25 cm. long, tight, closed by a brown to red membrane; inflorescence 10–15 cm. long, branching, pendent, 4–6 nodes, one spike per node, internodes 2–3 cm. long at the base shortening toward the apex, each node and peduncle enclosed by a leafy bract 1–30 cm. long, the lowest bracts being the longest; spikes androgynous except the terminal one which is staminate, 3–5 mm. wide, 5–10 cm. long, densely set with fruit, 7–8 ranks of perigynia around the axis; pistillate bracts oblong to obovate, 1.5–2 mm. wide, 3–4 mm. long, short-awned, three green to yellow nerves at the center, margins hyaline, brown to purple; staminate bracts lanceolate, 1 mm. wide, 4–5 mm. long, three center nerves yellow to brown, margins brown to purple; perigynia subspherical-ovoid or even ellipsoid, 2 mm. wide, 2.5 mm. long, lenticular, bi-convex in cross section with a distinct bulge giving one face more convexity than the other, two distinct ridges along the margins from the rostrum to the base, often a third along the bulge, rostrum shallowly bidentate, 5 mm. long, highly polished, smooth, obscurely nerved when immature, light brown to very dark brown; achenes obovoid, lenticular, glabrous to sparsely hirsute, minutely rugose, not filling the perigynium, yellow to brown; style 2–3 mm. long, doubled back against the achene and then passing out of the rostrum, splitting into two stigmas at the apex of the beak, glandular.

Distribution: Hawaii, Maui, Molokai, and Kauai in Zones D and E of Ripperton and Hosaka (1942), the middle and upper forest, in open places in the forest, along ditches and roadsides; common.

Type: U. S. South Pacific Exploring Expedition under the command of Capt. Wilkes, U. S. N., 1838–42, Sandwich Islands, Hawaii, *U. S. National Herb. No. 27224.*

Specimens examined

KAUAI: *Degener 2208,* Waineke Swamp, June 28, 1926, (NY); *Degener 2210,* Kokee Camp, June 25, 1926, (NY); *Fosberg 12674,* Plateau at the head of Kalalau Valley, 1250 m., Dec. 29, 1935; *Fosberg 12675,* Plateau at the head of Kalalau Valley, 1250 m., Dec. 29, 1935.

MOLOKAI: *Remy 148,* 1851–55, (GH); *Forbes 438.Mo,* Kolapamoa, Aug. 1912.

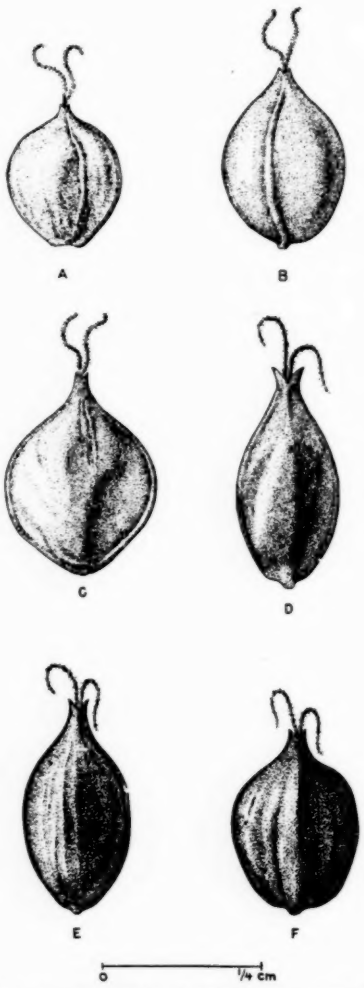

FIG. 17. Perigynia of *Carex alligata* F. Boott. *a, Degener 8251; b, Degener 2213; c, Krauss 481; d, Krauss 477; e* and *f, Fosberg 12675.*

MAUI: *Degener 8261,* Koolau Gap within Haleakala Crater, Aug. 17, 1928, (NY); *Degener 8256,* Olinda Pipe Line Trail, June 14, 1927, (NY); *Degener 8240,* Olinda Pipe Line Trail, July 30, 1927, (NY); *Degener 8251b,* Olinda Pipe Line, June 16, 1927, (NY); *Forbes 692.M,* Ukulele, July 1919; *Forbes 857a.M,* E of Ukulele, July 20, 1919; *Forbes 907.M,* Ukulele, July 1919; *Forbes 1168.M,* N slope of Haleakala, Aug. 17, 1919; *Hitchcock 14757,* Puu Kukui, Sept. 24–26, 1916, (US); *Hitchcock 14926,* E of Olinda, 4000′, Oct. 1, 1916, (US); *Krauss 338, 339, 340, 353,* Draw behind Paliku, 6500′, Sept. 3, 1948; *Krauss 386,* Olinda Dam end of Flume Line, 4400′, Sept. 6, 1948; *Krauss 388,* Olinda Flume Line, 4300′, Sept. 6, 1948; *Krauss 389,* road to Olinda Dam, 4400′, Sept. 6, 1948; *Krauss 395,* Olinda Flume Line, 4300′, Sept. 6, 1948; *Krauss 432,* trail above Haelaau, Puu Kukui, 3500′, Sept. 12, 1948; *Krauss 477,* trail above Haelaau, Puu Kukui, 3700′, Sept. 12, 1948; *Krauss 481,* trail above Haelaau, Puu Kukui, 4000′, Sept. 12, 1948; *Rock 8759,* Waikamoi Trail, May 14, 1911; *Rock 8761,* Waikamoi Trail, May 14, 1911; *St. John 10307,* Kula, Olinda Pipe Line, 4400′, Feb. 11, 1930.

HAWAII: *Degener 2212A,* 17 Mi. from Kohala toward Waimea, Aug. 1, 1926, (NY), (mixed collection); *Degener 2213,* 17 mi. trail from Kohala to Waimea, Aug. 14, 1926, (NY); *Degener 19411,* Popaloa, June 7, 1948, (NY); *Faurie 1221,* Mauna Kea, 2000 m., July 1909, (KY); *Faurie 1280,* Halawa, 800 m., June 1909, (KY); *Forbes 389.H,* Kau Desert, Aug. 2, 1911; *Forbes 803.H,* Hale Oloha, June 10, 1915; *Hillebrand 534,* (K); *Hitchcock 14378,* Waimea, Aug. 26, 1916, (US); *Mann & Brigham 325,* high central plateau, 1867, (G, US); *Remy,* (K); *Skottsberg 593,* forest above Pahala, 1000 m., Sept. 19, 1922, (GB); *St. John & R. S. Cowan & D. P. Rodgers 22400,* Saddle Road, Waiakea, S Hilo, 4000′, Dec. 26, 1946; *Wilkes Exped.,* 1838–42, (US); *Wilkes Exped.,* forest above sawmill, (K).

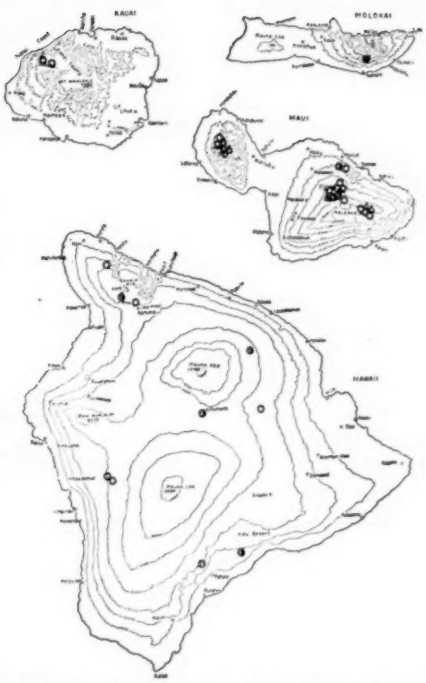

FIG. 18. Distribution of *Carex alligata* F. Boott (indicated by circles) and of *C. alligata* var. *Degeneri* R. Krauss (indicated by triangles).

Carex alligata Boott is a member of subgenus *Eucarex,* Coss. and Germ., section *Acutae* Fries, and subsection *Cryptocarpae* Tuckerman. It stands by itself within the group. Relationship of this species with the other *Cryptocarpae* in the islands is close but the characters separating them are clear. (See *Carex kauaiensis, Carex pluvia,* and *Carex pluvia* var. *koolauensis.*) The species seems to be an old one in the islands and the stock from which it sprang probably gave rise to the other two species and varieties. As mentioned before this group is a variable one and may be confusing. The young perigynia are a light yellow which sometimes turns to a very dark brown. This transition may be ob-

served by placing the perigynia in a moist petri dish for a few days. This variation in color may occur as in *Fosberg 12675* and *12674*, where all gradations may be seen on a single spike, or it may be found without intermediates, the perigynia being not only black or turning black but somewhat oval with exaggerated rostra, as in *Krauss 476, 479, 478*. The species responds with unusual sensitivity to the environment and may develop some of its different forms as a result of recombinations of one or more slightly different mutant genes affecting shape and surface of the perigynia.

Carex sandwicensis Boeck. based on *Remy 148*, Molokai, 1851–55 (G), is a later synonym published in 1875 and made by Boeckler apparently without knowledge of the earlier publication of Boott in 1867. It has been accepted and used widely but must be submerged.

Carex crustacea Nelmes, represented only by the type, is rather unusual in the great length of the internodes between the spikes and also in the reduced size of the spikes. The more normal internodes are 2–3 cm. long at the base and seldom as long above, as in Nelmes' *Carex crustacea*. It is believed from a study of the population that *Carex crustacea* cannot be maintained as a species. It is regrettable that at this stage in our science a species should be described from one fragmentary specimen and in a few vague words as a footnote to a key.

Carex Prescottiana Boott is illustrated in Boott's *Illustrations of the Genus Carex* from a collection of the U. S. Exploring Expedition (the Wilkes Expedition) from "the forest above the sawmill, Hawaii." The specimen secured from Kew has a note as follows:

> Laid in from herb. Boott, Oct. 1894. This is the whole Sandwich material which Boott *subsequently* pasted down in his type cover of *Carex Prescottiana*. From California Boott founded his *Carex Prescottiana* on Wall. Col. 3386 and published it in Proc. Linn. Soc., v. I, p. 280. When he got this material from Hawaii he determined it as identical with Wallich n. 3386 and then marked a query against Wallich's locality Nepal. I consider that the Hawaiian plant differs specifically from the Nepal one. It is *Carex sandwicensis*, Boeck.
>
> C. B. Clarke, Oct. 1894

All that remains of this specimen is a packet of one dozen loose fruits. On examination the black spots illustrated in Boott (1867: 45, Pl. 115) prove to be spots of a fungal infection. The veins shown in Boott's illustration are not found in all perigynia and in none as strongly as drawn. The two teeth of the rostrum are distinct in most of the fruits though the infected ones seem to be broken or missing. Clarke's conclusion is valid. The remaining specimens, however, do suggest a gradation into variety *Degeneri* which is found on Maui and Hawaii.

The type material which is figured by Boott is mentioned only as coming from the Wilkes Expedition collections in the district of Waimea, Hawaii. The material from the Wilkes Expedition marked *Carex alligata* Boott is now in the U. S. National Herbarium and is the only specimen which fits Boott's plate. The specimen, although it is the type, is not typical. It is a small young plant with somewhat narrower perigynia than those commonly found. Moreover, the perigynia have become dark although the typical surface persists.

Carex alligata Boott var. ***Degeneri*** var. nov.
Figs. 18, 19*a–b*

A specie differt in squamis foeminis purpureis aut purpureis-nigris in marginibus glabris aut albo-fimbriati carinis albis centralibus saepe aristatis, utriculis 1–2 mm. longis 2–5 mm. latis ovalibus aut ellipsoideis in lineamenta tenuiter biconvexis incorporis fulvis

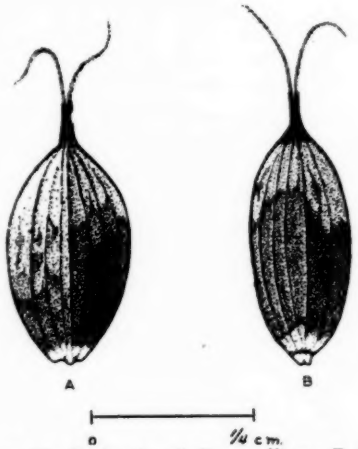

FIG. 19. Perigynia of *Carex alligata* F. Boott var. *Degeneri* R. Krauss. *a, b, Degener 8253.*

purpurei-maculosis, nervosis 5–8 gracilibus basis ad apicos extendentibus breve stipitatis apicibus rostrorum integris aut breve bidentatis oribus glabris aut setaciferis.

Vegetatively showing the same characters as the species but different in the following: pistillate bracts purple-black to black, smooth or white fringed on the margins, white-keeled through the center, prolonged in some to a setaceous awn; perigynia 1–2 mm. long, 3–5 mm. wide, narrow, oval to elliptic in outline, thinly bi-convex, surface yellow-brown splotched with purple, short stipitate, rostrum with an entire or weakly bidentate apex smooth or setaceous at the mouth, 5–8 thin nerves extending from base to the apex.

Type: Forbes 1189.M, Bog at Waianapanapa, Maui, Aug. 23, 1919.

Specimens examined

MAUI: *Degener 8253,* Mauka of Olinda on the way to Haleakala, June 15, 1927; *Forbes 1189.M,* Bog at Waianapanapa, Aug. 23, 1919; *Forbes 1226.M,* Waianapanapa, Aug. 23, 1919; *Fosberg 10026,* between Nakalalua and summit of Puu Kukui, 1740 m., Aug. 24, 1933.

This variety has a distinctly veined surface of the perigynium and an entire or slightly bidentate rostrum. There is a suggestion of the characteristic structure of the variety in certain other of the Maui specimens, especially those collected near Paliku, Maui, indicating a degree of transition. Individual plants give the impression of different species but the presence of intergradations makes a higher category impossible.

Carex kauaiensis sp. nov.

Figs. 20*a–c*, 21

Carex sandwicensis Boeck. f. *subverticillata* Kükenth. Fedde Rep. XVI, 435, 1920.

Rhizomatis caespitosis, squamis radicibus 8–10 mm. latis 2.5–11 cm. longis rubri-aut fusci-lineatis culmis fertilibus triangularis 2.4–4 mm. latis 120–150 cm. longis infra glabris supra scabris erectis, 4–8 laminis 13 mm. latis 150–200 cm. longis erectis in apicibus pendulis crassis in basis glabris in venosis et marginibus superioribus scabris, vaginis membranacis strictis 25 cm. altis deinde partitis inflorescentis 15–20 cm. longis 5–8 mm. latis ramosis 6–7 nodis unispiciferis internodis inferioribus 2–3 cm. longis superioribus brevioribus bractis laminiferi 2–4 mm. latis 3–30 cm. longis nodis inclusis, spicis androgynis praeter terminalis masculis 2–4 mm. latis 8–15 cm. longis pendulis laxe fructiferis utriculis vix basis utriculis superioribus contigendis, pedunculis 1–3 cm. longis ocreis 5–8 mm. longis striatis fissuratis inclusis, utriculis 3.5–6.5 mm. longis 1.5–2 mm. latis ellipsoideis aut obovoideis in rostro breve abrupte, coartato basi lata obtusa aut emarginata purpureis-nigris lucidibus scrobiculatis, costis tres ex rostris descendentibus ad basim et obscurantibus, achaenis obovoideis aureis rugosis triangularibus una latere latiora, stylis in 2 stigmatis 1 mm. supris rostris divisis.

Rootstocks caespitose; basal scales 8–10 mm. wide, 2.5–11 cm. long, streaked red or brown; fertile culm triagonal in cross section,

2.4–4 mm. wide, 120–150 cm. long, stiff, erect, smooth on the lower angles, lightly scabrous above; leaves 13 mm. wide, 150–200 cm. long, 4–8 per culm, erect, pendent at the ends, coarse, dark green, smooth at the base, becoming scabrous along the edges and main vein toward the apex; sheaths closed by a striate membrane to 25 cm. above the base, splitting at maturity, tight, holding the base as a slender unit; inflorescence branching, 15–20 cm. long, 5–8 mm. wide, 6–7 nodes per culm, one spike to a node, internodes 2–3 cm. at the base, shortening to 1 cm. at the apex, each node subtended by a leafy bract 2–4 mm. wide, 3–30 cm. long; spikes androgynous except the terminal one which is staminate, 2–4 mm. wide, 8–15 cm. long, pendent, sparsely set with fruit, the apex of one perigynium scarcely reaching the base of the next above it, peduncles 1–3 cm. long, enclosed by a striate, purple, split ochrea 5–8 mm. long; pistillate bract 1.5–2 mm. wide, 4–5 mm. long, ovate, short-awned, awn and three central veins white to yellow, membranous wings of the bract black to purple-black, waxy, awn 1–2 mm. long, toothed, broad; staminate bracts 1 mm. wide, 6–8 mm. long, lanceolate, short-awned, the awn toothed; perigynia 1.5–2 mm. wide, 3.5–6.5 mm. long, ellipsoid or broadly ellipsoid to obovoid, abruptly narrowed to the short 3–5 mm. bidentate rostrum, the base broad-obtuse or even emarginate, highly polished, black, finely scrobiculate surface with three obscure ridge lines equally radiating from the rostrum disappearing toward the base, triagonal in cross section; achenes obovoid, yellow, minutely rugose, triagonal in cross section, one side broader than the other two; style splitting into two stigmas 1 mm. above the rostrum, stigmas 1–2 mm. long, glandular, black.

Distribution: Kauai only, high bogs in Zones C_2 and D of Ripperton and Hosaka (1942), over 3,000 feet, in extremely wet open forest areas.

Type: Rock 9017, Kauluwehi Swamp, 4200′, Oct. 1909.

Specimens examined

KAUAI: *Degener 2208,* Waineke Swamp, Kokee, June 28, 1926, (NY); *Forbes 419.K,* Kaholuamano Swamp, Sept. 1909; *Forbes 885.K,* Alakai Swamp, Waimea Drainage Basin, West Side, July 3–Aug. 18, 1917; *Forbes 883.K,* Waimea Drainage Basin, West Side, Alakai Swamp; *Rock 9017,* Kauluwehi Swamp, 4200′, Oct. 1909; *Skottsberg 902,* forest near Alakai Swamp, Oct. 27, 1922, (GO); *St. John 23047,* Alakai Trail at BM 3698 3700′, Dec. 25, 1947; *St. John 23040,* Alakai Trail NE of second fork of Kawaikoi Stream, Dec. 25, 1947; *St. John 23041,* Alakai Trail 3900′, Dec. 25, 1947; *St. John 22926,* Ridge SW of Pihea, 4000′, Dec. 22, 1947.

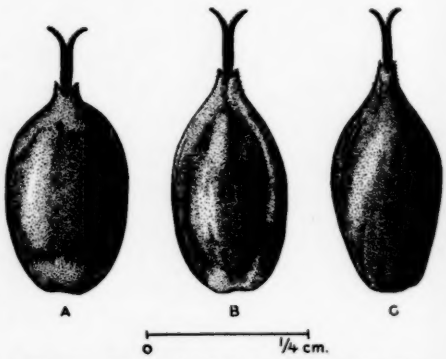

FIG. 20. Perigynia of *Carex kauaiensis* R. Krauss. *a, Rock 9017; b, Forbes 419.K; c, Skottsberg 902.*

Carex kauaiensis is a member of the subgenus *Eucarex,* section *Acutae,* subsection *Cryptocarpae.* It appears to be a recent species evolved from the line leading to *Carex alligata.* It differs from this in the pronounced smooth, polished, non-stipitate perigynium, the long-awned bracts, and the triagonal achene as well as the long internodes between points of perigynial attachment on the rachis.

FIG. 21. Distribution of *Carex kauaiensis* R. Krauss.

Kükenthal's description of forma *subverticillata* is, "Spiculae priores sed utriculi 2–4 fere verticillatum dispositi nigricomtes." He cites as his type *Rock 8017* with precisely the same data as those given on *Rock 9017* at the Bishop Museum. It is to be assumed that the 8 is a typographical error.

Dr. Carl Skottsberg has written that he also considers this a new species. He suggested the name *kauaiensis,* which is being adopted.

So far the species has been found only in the high bogs of Kauai. It is doubtful if it has spread to any other of the islands.

Nomen Inquirendum

Kükenthal (1909: 133) describes a new species, *Carex flaviceps,* collected on Oahu by Eschscholtz and deposited in the herbarium of the Botanical Garden in Leningrad, Russia. Requests for the loan of material from that source have not been answered. From the description the appearance of the plant is that of *Carex macloviana* except that it is androgynous and not gynaecandrous. Kükenthal mentions that the specimen is immature. The two characters are of primary importance in the subgenus *Vigneae* and one would not expect Kükenthal to make such a fundamental mistake. The locality, Oahu, also lends doubt to the supposition that the plant is *Carex macloviana.* Until such time as collections from the Russian herbaria are available the real identity of *Carex flaviceps* Kükenth. must remain a mystery.

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